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BY
STANLEY W. SZCZYTKO
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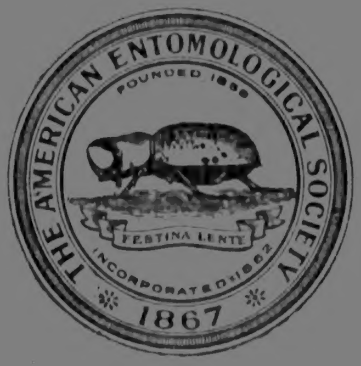

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STANLEY W. SZCZYTKO[2] AND KENNETH W. STEWART[3]

INTRODUCTION

The stonefly genus *Isoperla* was first established in 1906 when Banks split *Chloroperla* into *Isoperla, Alloperla* and *Chloroperla. Isoperla bilineata* (Say) was assigned as the genotype, and it was originally placed in the family Perlidae (Banks, 1906b, 1907a), although no type specimens were designated until 1978 (Szczytko and Stewart 1978). This classification scheme was accepted by early plecopterists, until 1940 (Needham and Claassen 1925, Claassen 1931, 1940).

Frison (1935) moved the *Isoperla,* as the subfamily Isoperlinae, into the Chloroperlidae, due to their lack of gills or gill remnants in nymphs and adults; presence of gills in nymphs is characteristic of all Perlidae. Seven years later, he proposed the group be given family status as the Isoperlidae since it was distinct from, but had characters in common with, both Perlidae and Perlodidae (Frison 1942).

Banks (1947) disregarded Frison's (1935, 1942) changes, and placed the *Isoperla* in the subfamily Isoperlinae (along with Chloroperlinae, Iso-

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geninae, Perlodinae, Calliperlinae and others) in the family Perlidae. He also split a number of *Isoperla* species into new genera, based upon antennae, head, femoral, wing, palpal and setal characteristics. Most important among these changes were: (1) *Perliphanes phaleratus* (Needham) was placed in the Perlodinae, (2) *Occiperla pinta* (Frison), *Calliperla luctuosa* (Banks) and others went into the Calliperlinae, (3) *Clioperla clio* (Newman), *Megahelus bellonia* (Banks) and others were assigned to the Isogeninae, and (4) *Nanoperla minuta* (Banks) = *Isoperla nana* (Walsh), *Walshioperla signata* (Banks), *Perliola quinquepunctata* (Banks) and all other *Isoperla* species into the Isoperlinae. Illies (1966), based on personal recommendation by W. E. Ricker in 1963, recombined all of these genera except *Calliperla* into *Isoperla.*

Ricker (1943, 1952), proposed that the Isoperlinae should be shifted from the Perlidae to Perlodidae, since the nymphs are separated from all other Perlidae by absence of thoracic gills and pointed paraglossae, and from the Chloroperlidae by the flatter nymphal body and 2-branched A_2 forewing veins that leave the anal cell separately. Recent workers have accepted this classification (Harden and Mickel 1952, Jewett 1959, 1960, Gaufin et al. 1966, 1972, Illies 1966, Zwick 1973, Hitchcock 1974, Szczytko and Stewart 1977, 1978, Baumann et al. 1977 and Surdick and Kim 1976). Ricker (1952) suggested that the Isoperlinae developed from an *Isogenus* ancestor, by reduction and loss of the supra-anal process, by movement of the ventral lobe from the 7th to the 8th sternum, and by modification of the paraprocts into hooks. He also indicated that the subfamily Isogeninae is most primitive, and the Perlodinae and Isoperlinae more specialized. The Isoperlinae shares absence of thoracic gills with the Perlodinae, and loss or reduction of the male epiproct with the Perlidae (Ricker 1952).

Illies (1966) included the genera *Calliperla* Banks, *Isoperla* Banks, *Mesoperlina* Klapalek and *Rickera* Jewett in the Isoperlinae (Perlodidae). Zwick (1973) added *Bulgaroperla* Rauser and *Kaszabia* Rauser to the subfamily.

As now classified, the Isoperlinae includes 3 Nearctic genera *Rickera, Isoperla* and *Calliperla.* We will propose a 4th North American genus *Cascadoperla* in this paper, to which is now assigned the single, distinct species *trictura* (Hoppe) (previously *Isoperla trictura*). The world and Nearctic *Isoperla* now number 125 and 57 species, respectively, and 21 are currently recognized from western North America. The other 68 species are from the Palearctic, making the genus exclusively holarctic.

Difficulties in classification in the group has, in part, been due to the morphological homogeneity among the *Isoperla* and the fact that no sus-

tained comparative study has been made of the genus. This problem has been recognized for a long time, and active world Plecopterists brought it forward as a high priority subject needing study, during the V and VI International Plecoptera Symposia in Washington, D.C., Sept., 1975 and Schlitz, West Germany, Aug., 1977. Because of this need and the exciting challenge offered by this interesting group of stoneflies, we have undertaken the difficult task of revision and study of the drumming behavior and biology of the Nearctic species. Several Plecopterists have given us encouragement, including S. G. Jewett who initiated serious study of the genus in the 1960's. Earlier, unpublished studies of *Isoperla* were made by J. F. Hanson in the 1940's. At present, separation of adults is often difficult, and in most cases nymphs have remained uncorrelated, and therefore undescribed or poorly described.

Our approach to this problem, of necessity, is one in at least two stages, due to size of *Isoperla*. This work represents the first of those stages, the study of the 21 western North American species. Our work over the past 5 years suggests that the eastern and western species probably have different origins in North America. Western nymphs have less distinct mouthparts and color patterns, and gravid females containing mature eggs are common in collections. The latter is not the case with eastern females, due apparently to some behavioral peculiarity of the life cycle, such as maturing of eggs while in the streamside forest canopy. We have maintained that the revision should include, as much as possible, comparative morphological characterization of all life stages and both adult sexes, according to arguments for holomorphological study in phylogeny by Henning (1966) and Ross (1974). This has necessitated rearing as many nymphs as possible, and a detailed SEM study of eggs of all species. Previous adult descriptions have not generally included analysis of the distinctive external and internal genitalia, and eggs of *Isoperla* have only been characterized as to shape, color and size for a few species (Knight, Nebeker, Gaufin 1965 a, b). This research is intended to serve as a foundation and model for eventual revision of the entire genus and subfamily.

Materials and Methods

In addition to extensive field studies, collection and rearing, over 5,000 *Isoperla* specimens from all known University, museum and individual sources were examined. Cooperating individuals and their University affiliations that loaned specimens were: Dr. R. W. Baumann, and Dr. S. L. Wood, Brigham Young Univ. (**BYU**); Dr. D. B. Donald, Canadian Wild-

life Service — Univ. of Calgary (**UC**); Dr. S. D. Smith, and Mr. D. Dunster, Central Washington State Univ. (**CWS**); Dr. J. V. Ward and Mr. L. J. Grey, Colorado State Univ. (**CSU**); Mrs. J. A. Schafrik, Cornell Univ. (**CU**); Dr. R. L. Newell, Idaho State Univ. (**ISU**); Dr. C. H. Triplehorn, Ohio State Univ. (**OSU**[1]); Dr. N. H. Anderson, Oregon State Univ. (**OSU**[2]); Dr. J. Linam, Southern Colorado State Univ. (**SCS**); Dr. P. H. Freytag, Univ. of Kentucky (**UK**); Dr. J. F. Hanson, Univ. of Massachusetts (**UM**[1]); Dr. A. R. Sheldon, Univ. of Montana (**UM**[2]); Dr. P. P. Harper, Univ. of Montreal (**UM**[3]); Mr. L. Dosdall, Univ. of Saskatchewan (**US**); Dr. A. R. Gaufin, and Mrs. R. Surdick-Pifer, Univ. of Utah (**UU**); Dr. G. F. Knowlton, Utah State Univ. (**USU**); Dr. W. Turner, Univ. of Washington (**UW**); and Mr. S. T. Elliott, Alaska Dept. of Fish and Game (**AFG**).

Curators and directors of major institutional museums that loaned specimens were: Dr. D. C. Rentz, California Academy of Sciences Museum (**CAS**); Dr. J. E. H. Martin, Canadian National Museum (**CNM**); Dr. D. W. Webb and Dr. J. Unzicker, Illinois Natural History Survey Museum (**INHS**); Dr. C. L. Hogue, Los Angeles County Museum of Natural History (**LCMNH**); Dr. P. Zwick, Max Planck Institute for Limnology (**MPIL**); Ms. M. K. Thayer, Comparative Zoology at Harvard Univ. (**MCZ**); Dr. O. S. Flint, Jr., Museum of Natural History, Smithsonian (**USNM**); and Dr. S. Rohwer, Thomas Burker Memorial Washington State Museum (**TBM**).

In addition, the following individuals loaned specimens from their extensive personal collections: Dr. B. P. Stark (**BS**), Mississippi College, Dr. R. W. Baumann (**RB**), Brigham Young Univ., Dr. W. E. Ricker (**WR**), Fisheries Research Board of Canada, Jr. L. J. Grey (**LG**), Colorado State Univ. Mr. S. G. Jewett (**SJ**), West Linn, Oregon, Mrs. R. Surdick-Pifer (**RP**), Univ. of Utah, Dr. J. A. Stanford (**JS**), North Texas State Univ., and Dr. D. G. Denning (**DD**), Moraga, California. Abbreviations for collections of the authors are Stanley W. Szczytko (**SWS**) and North Texas State Univ. (**NTSU**).

Field collecting trips were made to Colorado and New Mexico in Oct., Dec., 1974, and Jul., 1975. Two extensive trips, timed to coincide with full seasonal development of nymphs and/or emergence, were made in May, 1976, and May-Jun., 1977, to Colorado, New Mexico, Oregon, Utah, Washington, and Wyoming. Travel was supported by National Science Foundation Doctoral Dissertation Improvement Grant #DEB 76-15454 and the Faculty Research Fund of North Texas State University. Nymphs were collected live from selected and new localities for rearing and correla-

tion with adults. Successfully reared virgin adults were also utilized in a concurrent study of *Isoperla* drumming behavior.

Nymphs were maintained in 6-pac styrofoam containers, sometimes kept on ice in larger ice chests while in the field. Containers were checked daily, and correlated adults, exuviae, and nymphs were preserved in 70 percent ETOH or adults were temporarily utilized in dumming experiments.

The aedeagii of live males were everted just prior to fixing, by gently squeezing and rolling the abdomen between the thumb and forefinger, toward the posterior end. This provided better material for study, and saved the great amount of time and laborious procedure of extruding aedeagii of preserved specimens. This procedure is highly recommended to stonefly collectors, since spines and other sclerotized parts in some taxa often prevent successful, full eversion of the aedeagus in preserved specimens.

The aedeagii of preserved specimens were everted for study by the following method: (1) specimens were removed from alcohol preservative, placed in distilled H_2O and allowed to hydrate for approximately 5 min. (this step prevented the abdomen from rupturing when the KOH was heated), (2) they were then placed in a small beaker with 10 percent KOH and heated slowly over a hotplate until the specimen began to swirl, prior to boiling, (3) the specimen was allowed to rehydrate in distilled H_2O for 1 min. (the abdomen would often rupture from increased pressure if this time frame was not strictly followed), (4) the aedeagus was everted by placing a small bent "L-shaped" probe, made from a #1 insect pin behind the 9th sternum, directly below the cerci and paraprocts, then gently exerting a slight pressure by pushing another "L-shaped" probe posteriorly down the abdomen (extreme care must be taken at this point not to create too much internal pressure, which ruptures the aedeagal sac). In some cases this basic process was aided by teasing the unextruded lobes or spines until the hydrostatic pressure caused continued eversion, (5) after successful eversions, the abdomen was clipped from the body for ease of positioning and examination. Shape and location of the aedeagus, its patterns of spinulae, and sclerotized structures were studied critically at 187.5× using a Wild M5 Steromicroscope on Dark Field Base, fitted with a 2× objective converter, and drawn using a Wild Drawing Attachment.

Steps 1-3 above were followed in preparing females for study of internal genitalia. The vaginal cavity, spermatheca, receptacular duct and accessory glands were then carefully dissected out for study and illustration.

Mature ova from preserved gravid females were prepared for SEM study by the following method: 1. they were sonicated in a small BEEM[R] capsule containing 90 percent ETOH for 1.5 min., using an E/MC RAI ultrasonic cleaner, 2. sonicated ova were kept in 100 percent ETOH for approximately 20 min., transferred to 90 percent amyl acetate for 15 min., then kept in 100 percent amyl acetate for 10-12 min., 3. they were then individually air dried on the tips of light-touch forceps, and then attached to an aluminum specimen stub, using Scotch brand double stick tape No. 292-030, 4. stubs were coated with ca. 200 Å of gold, using a Film-Vac Mini-Coater EMS-41 for 2 min. at a voltage of 10 milliamps.

Prepared ova were studied using an International Scientific Instruments Mini-SEM 151 scanning electron microscope. Views of micropyles, chorionic sculpturing and reticulations, attachment structures, collar areas, and whole ova were photographed at several magnifications. Occasionally, when circumstances and time allowed, ova from live females were placed in a depression cell with distilled H_2O, and studied with a Zeiss Model 4721816 light microscope. This was helpful in interpreting any size and shape changes due to preservation, and nature and proliferation of the gelatinous matrix when first placed in H_2O (simulated oviposition).

Nymphs whose mouthparts and proventriculi were to be studied, were prepared according to the aedegii study steps 1-3 outlined above. These parts were then dissected out, using minuten pin probes and scalpels, placed in 80 percent ETOH, then transferred directly to a slide mount using Hoyer's Mounting Medium #37W9700. The paraglossae, glossae, mentum, submentum, maxillae, mandibles, and labrum were drawn with the Wild M-5 and camera lucida. Size, shape, and number of rows of proventricular teeth were photographed with the Zeiss Photomicrography setup. Nymphal head-pronotum pigment patterns and tergal setation were drawn.

Acknowledgments

The authors wish to acknowledge Dr. R. W. Bauman, Dr. Bill P. Stark, Dr. W. E. Ricker, Peggy Szczytko and John Fraley for helpful suggestions during manuscript preparation.

Results

Systematic List of Western Nearctic *Isoperla* Species Complexes and the Monotypic *Cascadoperla,* According to Holomorphological Relationships.

Genus *Isoperla*

I. quinquepunctata complex:	*I. jewetti* Szczytko and Stewart, *I. longiseta* Banks, *I. mormona* Banks, *I. quinquepunctata* (Banks).
Unassigned species	*I. katmaiensis* (new species)
I. phalerata complex:	*I. phalerata* (Needham), *I. pinta* Frison.
I. sobria complex:	*I. sobria* (Hagen), *I. gravitans* (Needham and Claassen), *I. tilasqua* (new species).
I. marmorata complex:	*I. fulva* Claassen, *I. marmorata* (Needham and Claassen).
I. sordida complex:	*I. acula* Jewett, *I. adunca* Jewett, *I. bifurcata* (new species), *I. denningi* Jewett, *I. fusca* Needham and Claassen, *I. petersoni* Needham and Christenson, *I. rainiera* Jewett, *I. sordida* Banks.

Genus *Cascadoperla* (new genus)

C. trictura complex:	*C. trictura* (Hoppe)

Keys to the Western Nearctic Cascadoperla and Isoperla

Adult Males

1. Tenth tergum partially cleft, genital hooks developed from posterior margin of 10th tergum, paraprocts blade-like, weakly sclerotized, rounded at tips, not attached to base of cerci (Figs. 230 & 234) ..... *Cascadoperla trictura*

   Tenth tergum entire, genital hooks developed as sclerotized, modified paraprocts pointed or blunt at tips, and attached to base of cerci ..... *Isoperla* (2)

2.(1). Pronotum checkered black on yellow, paraprocts with blunt tips and acute ventral spine (Figs. 58 & 80) ..... (3)

   Pronotum not checkered black on yellow, paraprocts variable, usually without ventral spine ..... (4)

3.(2). Ninth tergum with bipartite mesal patch of stout spinulae (Fig. 59), apex of aedeagus without scattered long hair-like spinulae (Fig. 62) ..... *I. phalerata*

   Ninth tergum with entire mesal band of stout spinulae (Fig. 78), apex of aedeagus with scattered long hair-like spinulae (Fig. 81D) .... *I. pinta*

4.(2). Aedeagus completely membranous ..... (5)

   Aedeagus bearing a variable sclerotized process ..... (12)

5.(4). Ninth and/or 10th terga bearing bipartite patches of long stout setae or short spinulae ..... (6)

   Ninth and 10th terga devoid of long stout setae or spinulae ..... (10)

6.(5). Ninth and 10th terga bearing bipartite mesoposterior patches of long stout setae (Fig. 31), aedeagus with 2 large mesolateral lobes bearing small fine spinulae ..... *I. quinquepunctata*

Ninth tergum bearing bipartite mesoposterior patch of long stout setae or spinulae, 10th tergum void of spinulae, or stout setae, aedeagus without 2 large mesolateral lobes ..... (7)

7.(6). Vesicle truncate (Fig. 23), paraprocts short and stout (Figs. 25 & 26), apex of aedeagus tube-like bearing fine spinulae (Fig. 28) .... *I. mormona*

Vesicle not truncate, paraprocts elongate and tapered, apex of aedeagus not tube-like ..... (8)

8.(7). Wings macropterous, apex of aedeagus with 2 anterodorsal, and 2 posterodorsal rounded lobes and 2 short posterior tubular processes (Fig. 7) ..... *I. longiseta*

Wings brachypterous, apex of aedeagus without paired dorsal lobes and tubular processes elongate ..... (9)

9.(8). Interocellar area of head dark (Fig. 38), vesicle petiolate (Fig. 39), aedeagus with 2 long dorsal tubular processes (Fig. 41) .... *I. katmaiensis* (new species)

Interocellar area of head light, vesicle broadly rounded posteriorly, wide at base, aedeagus with a single long dorsal tubular process .... *I. jewetti*

10.(5). Vesicle obsolescent, paraprocts tapering to long fine tips, (Figs. 90 & 91), aedeagus with one band of long hair-like spinulae (Fig. 85), apex bearing 2 pointed lobes (Fig. 85) ..... *I. sobria*

Vesicle developed, paraprocts short, aedeagus with 2 or no bands of hair-like spinulae, apex not bearing 2 pointed lobes ..... (11)

11.(10). Pronotum with 2 wide, dark concolorous, longitudinal bands bordering median light stripe, rugosities absent (Fig. 105), vesicle lighter than rest of 8th sternum (Fig. 106), aedeagus without long hair-like spinulae (Figs. 109 & 110) ..... *I. gravitans*

Pronotum light brown with dark brown rugosities and median light stripe (Fig. 112), vesicle darker than rest of 8th sternum (Fig. 113), aedeagus with 2 posterior patches of long hair-like spinulae (Figs. 115 A & D) ..... *I. tilasqua*

12.(4). Vesicle wide at base and broadly rounded, dorsal arm of sclerotized aedeagal process not forked, club-shaped bearing various small spines at apex ..... (13)

Vesicle variable and stalked, dorsal arm of sclerotized aedeagal process forked, not club-shaped ..... (12)

13.(12). Paraprocts long and tapered, recurving over 10th tergum (Fig. 122), apex of aedeagus enlarged bearing large rounded spinulae (Fig. 123E), sclerotized process flattened laterally, blade-like (Fig. 123D) .... *I. marmorata*

Paraprocts short, stout not recurving over 10th tergum (Figs. 140 & 142), apex of aedeagus with 2 large conical lobes mostly spinule free (Fig. 138), sclerotized process not flattened laterally, tip ladle-like (Fig. 138F) ..... *I. fulva*

14.(12). Interocellar area of head mostly dark, never entirely light ..... (15)

Interocellar area of head entirely light ..... (18)

15.(14). Paraprocts thin, long, narrow, tapering to long fine point (Fig. 223), sclerotized aedeagal process forked, arms short and rounded, tips

bearing row of small stout pines (Figs. 222 & 225E) ..... *I. sordida*
Paraprocts variable, not elongate and finely tapered, dorsal arm of sclerotized aedeagal process unforked and variable ..... (16)

16.(15). Vesicle narrow at base and lateral margins parallel (Fig. 158), head pattern light between ocellar triangle and base of antennae (Fig. 157), sclerotized process of the aedeagus small, short, rod-like, slightly expanded at tip (Fig. 160D) ..... *I. adunca*
Vesicle petiolate, median brown pigment band connecting base of antennae to ocellar triangle, sclerotized process of aedeagus variable, not rod-like ..... (17)

17.(16). Paraprocts stout, deflected downward at apex to sharp points, (Fig. 205), dorsal arm of sclerotized aedeagal process developed into single long, curved, tapered, needle-like process (Fig. 207C) ..... *I. petersoni*
Paraprocts wide at base, tapering to short fine tips, not deflected downward at tips (Figs. 215 & 216), dorsal arm of sclerotized aedeagal process short, stout, apex expanded with 2 sharp lateral downward deflecting spines (Figs. 214 & 218D) ..... *I. rainiera*

18.(14). Mesoposterior margin of 9th tergum bearing patch of stout barrel-like spinulae and long fine hairs (Fig. 156), vesicle rectangular (Fig. 154) ..... *I. acula*
Mesoposterior margin of 9th tergum devoid of spinulae and long hairs, vesicle variable, not rectangular ..... (19)

19.(18). Dorsal arms of forked sclerotized aedeagal process short and rounded (Figs. 181 & 183C), vesicle with lateral margins parallel, rounded posteriorly (Fig. 184) ..... *I. denningi*
Dorsal arms of forked sclerotized aedeagal process long and pointed at tips, vesicle variable, lateral margins not parallel ..... (20)

20.(19). Vesicle truncate (Fig. 164), dorsal arms of sclerotized aedeagal process not extending beyond length of base, tips with ventral spine (Figs. 165C & 168) ..... *I. bifurcata*
Vesicle not truncate, expanding apically and evenly rounded posteriorly (Fig. 187), dorsal arms of sclerotized aedeagal process extending well beyond length of base (Figs. 189 & 191C), curled blunt ventral spine near fork, crossed near tips ..... *I. fusca*

Adult Females*

1. Subgenital plate reduced to a small mesoposterior nipple (Fig. 235), complete median dark stripe on head, darkest between ocelli, pronotum with median light stripe and 2 narrow longitudinal dark bands bordering it (Fig. 228) ..... *Cascadoperla trictura*
Subgenital plate produced and variable, head-pronotal patterns variable, without complete median stripe on head ..... *Isoperla* (2)

2.(1). Pronotum checkered black on yellow, subgenital plate broadly rounded posteriorly with a median notch ..... (3)
Pronotum not checkered black on yellow, subgenital plate variable .... (4)

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*Females of *I. acula* are unknown.

3.(2). Dark band of ocellar triangle not connected between lateral ocelli, posterior margin of head completely light, (Fig. 56), subgenital plate slightly angulate (Fig. 61), cross veins usually present in the branches of the radial sector of forewings (Fig. 60) ..... *I. phalerata*

Dark band of ocellar triangle connected at lateral ocelli, posterior margin of head with median band connected to base of ocellar triangle (Fig. 75), subgenital plate broadly rounded not angulate (Fig. 79), cross veins absent from branches of the radial sector of forewings, (Fig. 82) ..... *I. pinta*

4.(2). Subgenital plate elongate, lateral margins parallel ..... (5)

Subgenital plate variable, lateral margins not parallel ..... (6)

5.(4). Pronotum with 2 wide dark concolorous longitudinal bands bordering median light stripe, rugosities absent (Fig. 105), subgenital plate lighter than rest of 8th sternum, light pigmentation extending to base of 8th sternum forming "V"-shaped pattern, 2 sclerotized patches on inner surface at posterolateral margins (Fig. 111) ..... *I. gravitans*

Pronotum median brown with dark brown rugosities and median light stripe (Fig. 112), subgenital plate not lighter than rest of 8th sternum, light "V"-shaped pattern and sclerotized patches absent (Fig. 117) ..... *I. tilasqua*

6.(4). Interocellar area mostly dark, never entirely light ..... (7)

Interocellar area entirely light ..... (11)

7.(6). Head pattern mostly light except for dark solid ocellar triangle (Fig. 157), subgenital plate slightly triangular with deep mesoposterior notch (Fig. 161) ..... *I. adunca*

Head pattern variable, not mostly light, subgenital plate variable not slightly triangular ..... (8)

8.(7). Pronotal rugosities distinctly rounded (Fig. 38), subgenital plate semicircular without mesoposterior emargination (Fig. 43) .... *I. katmaiensis* (new species)

Pronotal rugosities irregular, not distinctly rounded, subgenital plate not semicircular ..... (9)

9.(8). Subgenital plate without mesoposterior emargination, posterolateral margins of 8th sternum with dark brown spots (Fig. 217) ..... *I. rainiera*

Subgenital plate with mesoposterior emargination, posterolateral margins of 8th sternum without dark brown spots ..... (10)

10.(9). Subgenital plate with deep mesoposterior emargination, base distinct from posterolateral margins of 8th sternum (Fig. 209) ..... *I. petersoni*

Subgenital plate with shallow mesoposterior emargination, base not distinct from posterolateral margins of 8th sternum (Fig. 224) .... *I. sordida*

11.(6). Subgenital plate semicircular or nearly so ..... (12)

Subgenital plate not semicircular or nearly so ..... (14)

12.(11). Dark bands of ocellar triangle connected to base of antennae by a wide dark band (Fig. 84), large, dark species ..... *I. sobria*

Dark bands of ocellar triangle not connected to base of antennae by a wide dark band, small light species ..... (13)

13.(12). Pronotum evenly suffused with brown except for median light stripe, (Fig. 22), subgenital plate shallow, broadly rounded (Fig. 27) .....

..... *I. mormona*

Pronotum not suffused with brown, light with dark brown rugosities and median light stripe (Fig. 3), subgenital plate produced, semicircular or truncate (Fig. 9) ..... *I. jewetti* & *I. longiseta*

14.(11). Subgenital plate triangular or nearly so ..... (15)

Subgenital plate broadly rounded ..... (17)

15.(14). Subgenital plate without mesoposterior emargination usually with median nipple (Fig. 139, 141, & 144), dark bands of ocellar triangle connected to base of antennae by wide dark brown "M"-shaped dark band (Fig. 135) ..... *I. fulva*

Subgenital plate with mesoposterior emargination, dark bands of ocellar triangle not connected to base of antennae by "M"-shaped dark band ..... (16)

16.(15). Subgenital plate usually with a deep wide mesoposterior notch, produced 1/4 length of 9th sternum (Fig. 37), abdominal segments usually with a red cast ..... *I. quinquepunctata*

Subgenital plate with a shallow mesoposterior emargination produced 1/2 length of 9th sternum (Fig. 180), abdominal segments without a red cast ..... *I. denningi*

17.(14). Subgenital plate slightly produced, evenly rounded (Fig. 124), anal area of hindwings fumose ..... *I. marmorata*

Subgenital plate produced 1/4 length of 9th sternum with slight mesoposterior emargination, anal area of hindwings not fumose .... *I. fusca* & *I. bifurcata*

Nymphs*

1. Occiput with transverse spinule row ..... (2)

Occiput without transverse spinule row ..... (9)

2.(1). Interocellar area dark ..... (3)

Interocellar area light ..... (6)

3.(2). Laciniae with bush of long stout hairs and 3 stout spines on elevated ridge below subapical tooth (Fig. 233), numerous long hairs irregularly placed on lateral and posterior margins of pronotum (Fig. 229) .... *Cascadoperla trictura*

Laciniae without elevated ridge, bush of long hairs and 3 stout spines below subapical tooth, few scattered long hairs irregularly placed on lateral and posterior margins of pronotum ..... (4)

4.(3). Femora, tibiae, and tarsi without dorsal fringe of long fine hairs (Fig. 190), meso- and meta-nota with 4 longitudinal dark brown stripes, 2 bordering median light stripe and 2 lateral (Fig. 186) ..... *I. fusca*

Femora, tibiae and tarsi with dorsal fringe of long fine hairs, meso- and meta-nota without 4 longitudinal dark brown stripes ..... (5)

5.(4). Light "U"-shaped area beyond anterior ocellus, wide longitudinal medium brown bands with variable light areas bordering light median stripe of pronotum (Fig. 206) ..... *I. petersoni*

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*Nymphs of *I. acula, I. adunca, I. bifurcata, I. denningi, I. gravitans, I. katmaiensis, I. sordida* and *I. tilasqua* are unknown.

Light "U"-shaped area beyond anterior ocellus usually absent, longitudinal dark brown bands bordering light median stripe of pronotum entirely dark without light areas (Fig. 137) ..... *I. fulva*

6.(2). Pronotum wider than head, angles strongly rounded (Fig. 63) .... *I. phalerata*

Pronotum not wider than head, angles moderately rounded ..... (7)

7.(6). Cerci without a continuous dorsal fringe of long fine hairs after segment 17, head pattern mostly light except for 2 quadrangular dark brown patches connecting lateral ocelli with anterior ocellus (Fig. 5) .... *I. jewetti* & *I. longiseta*

Cerci with a continuous dorsal fringe of long fine hairs after segment 17, head pattern with medium brown patches connecting base of head to lateral ocelli and anterior ocellus with base of antennae ..... (8)

8.(7). Pronotum mostly light except for 2 light brown bands near lateral margins, distinct light median stripe absent (Fig. 32) .... *I. quinquepunctata*

Pronotum medium brown with 2 wide dark longitudinal bands with variable light areas bordering light median stripe (Fig. 5) .... *I. mormona*

9.(1). Interocellar area completely dark ..... (10)

Interocellar area partially light ..... (11)

10.(9). Pro-, meso- and meta-thoracic sterna with median patches of long golden brown setae (Fig. 211), pronotal rugosities present (Fig. 212), femora, tibiae, and tarsi without fringe of long dorsal hairs (Fig. 219) ..... *I. rainiera*

Pro-, meso- and meta-thoracic sterna without median patches of long golden brown setae, pronotal rugosities absent (Fig. 120), tibiae and tarsi with fringe of long dorsal hairs ..... *I. marmorata*

11.(9). Pronotum checkered black on yellow, upper and lower angles with a few irregularly placed long hairs (Fig. 77), dark brown band on femora near distad ..... *I. pinta*

Pronotum with 2 wide longitudinal suffused brown bands, not checkered, upper and lower angles without a few irregulaly placed long hairs (Fig. 86), distad of femora without dark brown band ..... *I. sobria*

Ova*

1. Collar absent ..... (2)

Collar present ..... (3)

2.(1). Cross section triangular except circular at poles, chorionic ridges elevated forming hexagonal cells, appearing reticulate (Figs. 173 & 174) .... *I. adunca*

Cross section entirely circular, chorionic ridges elevated forming deep irregular shaped depressions, not appearing reticulate (Figs. 193-195 & 200) ..... *I. bifurcata*

3.(1). Chorion entirely smooth (Figs. 47-49) ..... *I. katmaiensis*

Chorion sculptured not smooth ..... (4)

4.(3). Cross section a 9-sided polygon, chorion striate (Figs. 44-46 & 50) .... *Cascadoperla trictura*

*Ova of *I. acula* are unknown.

Cross section circular or partially triangular not 9-sided, chorion not striate ..... (5)

5.(4). Chorionic ridges absent or developed slightly, not elevated ..... (6)
Chorionic ridges well developed, variable and elevated ..... (12)

6.(5). Base of collar set in a wide circular depression bordered by a low ridge, and void of chorionic sculpturing (Figs. 93, 94, & 96) ..... *I. sobria*
Base of collar not set in a wide circular depression void of sculpturing ..... (7)

7.(6). Cross section of anterior 1/2 triangular (Fig. 15) ..... *I. quinquepunctata*
Cross section entirely circular ..... (8)

8.(7). Chorionic ridges evident but not elevated ..... (9)
Chorionic ridges not evident ..... (10)

9.(8). Collar expanded at apex (Figs. 10, 11 & 13), micropyles small, arranged in pairs (Figs. 11 & 17) ..... *I. mormona*
Collar not expanded at apex (Figs. 68, 69, & 71), micropyles large, arranged in threes (Fig. 70) ..... *I. phalerata*

10.(8). Micropyles minute without sperm guides or grooves (Fig. 170) *I. denningi*
Micropyles normal size with grooves and sperm guides ..... (11)

11.(10). Collar well developed and elevated (Figs. 18 & 21) ..... *I. longiseta*
Collar depressed not elevated ..... *I. jewetti*

12.(5). Micropyles ornate, highly elevated with one to several openings (Figs. 65 & 66) ..... *I. pinta*
Micropyles not ornate and highly elevated, with only one opening .... (13)

13.(12). Chorionic ridges narrow forming distinct hexagonal shaped cells ..... (14)
Chorionic ridges thickened forming variable shaped depressions ..... (17)

14.(13). Micropyles arranged on elevated transverse polar ridges near bottom 1/3 ..... (15)
Micropyles not arranged on elevated transverse polar ridges near bottom 1/3 ..... (16)

15.(14). Micropyles arranged on thickened polar ridge elevated above chorionic ridges, sperm guides absent (Fig. 73), collar distinct, crown-like (Figs. 72 & 74) ..... *I. petersoni*
Micropyles arranged on polar ridge not elevated above chorionic ridges, sperm guides present and elongate (Fig. 202), collar not distinctly crown-like (Figs. 201 & 203) ..... *I. sordida*

16.(14). Collar reduced (Fig. 197), micropyles minute, arranged singularly (Figs. 198 & 199) ..... *I. fusca*
Collar well developed (Figs. 101 & 104), micropyles enlarged with a small groove preceding each opening, arranged in pairs (Fig. 103) ..... *I. tilasqua*

17.(13). Collar developed slightly (Fig. 176) ..... *I. rainiera*
Collar well developed ..... (18)

18.(17). Chorionic ridges greatly thickened, fused and not distinct (Figs. 128-130) ..... *I. fulva*
Chorionic ridges distinct, not fused ..... (19)

19.(18). Collar with elevated circular ridge at base (Figs. 97 & 100), chorionic depressions shallow (Figs. 97-99) ..... *I. gravitans*
Collar without elevated circular ridge at base (Figs. 125 & 126), chorionic depressions deep (Figs. 125-127) ..... *I. marmorata*

Genus ISOPERLA Banks

Chloroperla, Pictet, 1841:276. Syn. Banks 1906.
Isoperla Banks 1906 b, 17:175. (Type species: *Isoperla bilineata* (Say). Syn. indicated.
Suzukia Okamoto, 1912, 4:109. Syn. Ricker 1952.
Megahelus Klapalek, 1923, 63:24. Syn. Claassen 1940.
Clioperla Needham and Claassen, 1925, 2:137. Syn. Frison 1935.
Isoperla, Frison, 1935, 20:428. Syn. indicated.
Isoperla, Claassen, 1940, 232:197. Syn. indicated.
Perliphanes Banks, 1947, 54:278. Syn. Ricker i. 1. 1963.
Occiperla Banks, 1947, 54:280. Syn. Ricker i. 1. 1963.
Nanoperla Banks, 1947, 54:283. Syn. Ricker i. 1. 1963.
Walshiola Banks, 1947, 54:283. Syn. Ricker i. 1. 1963.
Perliola Banks, 1947, 54:284. Syn. Ricker i. 1. 1963.
Isoperla, Ricker, 1952, 18:142. Syn. indicated.
Isoperla, Illies, 1966:392.
Isoperla, Zwick, 1973:240.

WESTERN NEARCTIC SPECIES

Adult-Body length: small to medium (5-18 mm). Wings: macropterous or brachypterous, clear or fumose, fork of 2nd anal vein of forewings included in anal cell so that its branches leave the cell separately. Gills: absent from thorax or abdomen. Pronotum: variable median light stripe. Mesosternum: arms of "Y"-shaped mesosternal ridge attached to posterior end of furcal pits, transverse ridge connecting anterior tips of furcal pits. Body color: variable light yellow to dark brown. Abdominal terga: usually with 3 longitudinal dark stripes, one mesal and 2 lateral.

Male terminalia-Ninth tergum: with or without patches of stout spinulae or long stout setae. Tenth tergum: entire, with or without patches of stout spinulae or long stout setae. Vesicle: variably shaped, usually developed at mesoposterior margin of 8th sternum (obsolescent in *I. ebria*). Paraprocts: sclerotized, variable, usually recurving forward to level of or over 10th tergum. Aedeagus: variable, entirely membranous or with variable sclerotized processes, bearing variable sized and shaped spinulae.

Female terminalia-Subgenital plate: developed on posterior margin of 8th sternum, variable shaped from evenly rounded to triangular. Vagina: lined with variable shaped spinulae, 6-7 long tubular accessory receptacular glands attached to seminal receptacle or receptacular duct, receptacular duct long, tubular, seminal receptacle variable shaped membranous sac.

Nymphs-Body length: small to medium (7-16 mm). Body color: light yellow to dark brown. Pronotum: median light stripe (indistinct in *I. quinquepunctata*), margins fringed entirely with short stout hairs and, usually a few long hairs. Gills: absent from submentum, thorax and abdomen. Maxilla: lacinia with apical and subapical teeth, inner margin with a row of long stout hairs, maxillary palpus 5-segmented. Labrum: mesoanterior margin with nipple or small hump. Mandible: 6 teeth, inner margin with bush of long stout hairs below apical tooth. Labium: labial palpus 3-segmented, paraglossae much larger than glossae usually with small apical nipple. Mesosternum: arms of "Y"-shaped mesosternal ridge attached to

posterior end of furcal pits, transverse ridge connecting anterior tips of furcal pits. Proventriculus: 23-26 variable longitudinal rows of stout, posterior projecting spinulae. Abdominal terga: usually with 3 longitudinal dark stripes, one mesal and 2 lateral.

Ova-Cross section: circular to triangular. Collar: variable, usually developed and expanded (absent in *I. adunca* and *I. bifurcata*). Chorion: usually sculptured (smooth in *I. katmaiensis*). Micropyles: variable in number arranged near bottom 1/3 on one side.

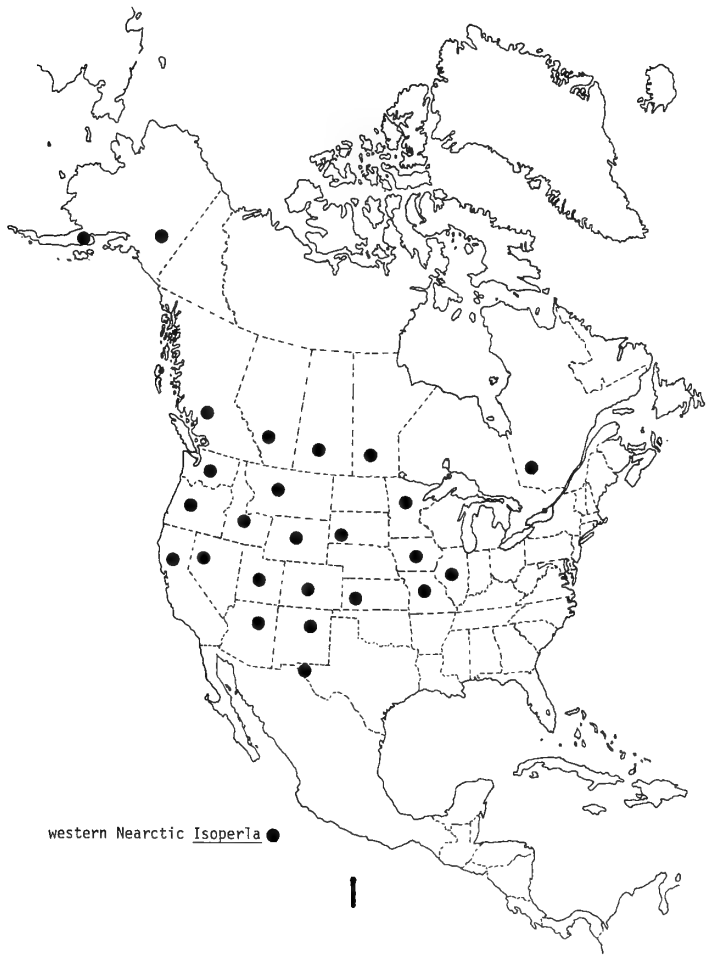


FIGURE 1. — Distribution of western Nearctic *Isoperla*.

Diagnosis and Discussion. — *Isoperla* is most similar to *Rickera* Jewett, and they share the following characters: 1. entire male 10th tergum, 2. absence of male supraanal process, 3. male paraprocts developed into genital hooks and attached to base of cerci (genital hooks not developed from 10th tergum), 4. fork of 2nd anal vein of forewings included in the anal cell so that its branches leave the cell separately, 5. lack of gills or gill remnants in nymphs and adults, 6. arms of the "Y"-shaped mesosternal ridge attached to posterior end of furcal pits in adults and nymphs, 7. wide median light stripe on adult and nymphal pronotum, and 8. usually three dark longitudinal stripes on nymphal abdominal terga, one narrow mesal, and 2 wide lateral. *Rickera* differs from *Isoperla* by having the male vesicle on the 7th rather than the 8th sternum, paraprocts are mostly membranous, and the nymphal lacinia bears only one apical tooth. Males of *Isoperla* differ from the Perlodinae in that the vesicle is on the posterior margin of the 8th sternum rather than the 7th.

The genus is widely distributed throughout the western cordillera, occurring from Texas to Alaska and Illinois to California (Fig. 1). The species inhabit all types of lotic systems, and emergence begins in late spring and continues throughout the summer. Most species are thought to undergo univoltine life cycles.

The name of each following western *Isoperla* species group is based on its earliest valid species representative.

SPECIES GROUP A

Isoperla quinquepunctata complex

This group is composed of *I. jewetti* Szczytko and Stewart, *I. longiseta* Banks, *I. mormona* Banks and *I. quinquepunctata* (Banks). *I. patricia* Frison is not included here, since all morphological evidence and drumming behavior (unpublished concurrent study) indicate that it is a synonym of *I. quinquepunctata.* These species all share the following characteristics: 1. male with entirely membranous aedeagus, bearing patches, or bands of small stout, or small fine spinulae, 2. 9th and/or 10th male abdominal terga with patches of long stout hairs or spinulae, 3. female subgenital plate broadly rounded posteriorly, but variable and sometimes similar to females of other groups, 4. ova with well-developed collar and relatively smooth chorion, having small punctations, and ridges reduced or absent; lower 1/3 of egg with micropyles arranged in groups of 2 or 3, only on one side, 5. faint row of occipital spinulae on nymphal head, 6. nymphal femora, tibia and tarsus with a dorsal fringe of long hairs, and 7. three longitudinal stripes on abdominal terga.

The group is widely distributed from Illinois to California and Texas to Canada (Fig. 2). *I. longiseta* and *I. jewetti* mainly inhabit large rivers, *I. quinquepunctata* is found in small rivers and creeks, and *I. mormona* is found in creeks and larger rivers. The species exhibit a seasonal emergence succession with *I. quinquepunctata* beginning in early May, especially in more southern latitudes, and *I. longiseta* and *I. mormona* extending until late Jun.-Aug. All species are thought to undergo univoltine life cycles.

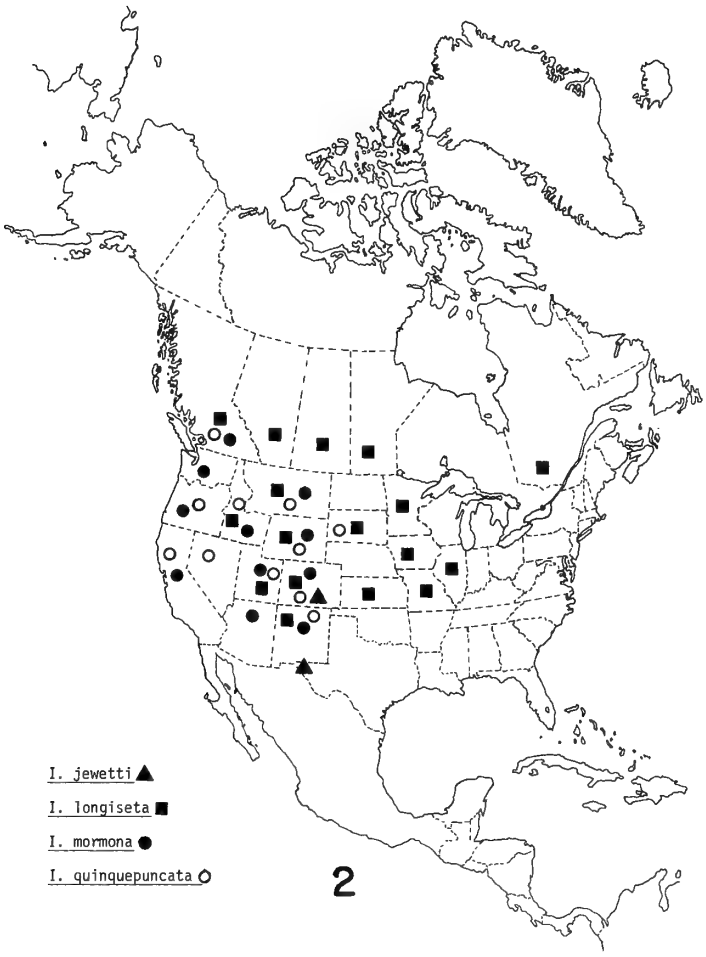


FIGURE 2. — Distribution of the *I. quinquepunctata* complex.

Isoperla jewetti Szczytko and Stewart

Isoperla longiseta, Frison, 1942, 22:318. In part.
Isoperla jewetti Szczytko and Stewart, 1976, 36:215. Holotype ♂, and Allotype ♀; 5-10 mi. S. of El Paso, on rd. to Marathon, El Paso Co., Texas, USA, (INHS) (male and female genitalia, aedeagus, nymphal mouthparts, and ova).
Isoperla jewetti, Szczytko and Stewart, 1977, 103:355 (male and female genitalia, aedeagus, nymphal mouthparts, and ova).

Male. — Brachypterous. Length of forewings 1.5-2.0 mm; length of body 6-7 mm. General body color light brown. Head-pronotal pigment pattern similar to *I. longiseta* (Fig. 3). Ninth tergum with bipartite patch of stout setae and dark brown pigmentation. Tenth tergum with 2 dark brown patches void of setae at posterior margin (Szczytko and Stewart 1976; Fig. 10). Vesicle, broader at base than apex (Szczytko and Stewart 1976; Fig. 9). Paraprocts slender, tapering to points apically, and recurving anteriorly, slightly over 10th tergum (Szczytko and Stewart 1976; Figs. 10 & 11). Aedeagus entirely membranous with long dorsal finger-like process (Szczytko and Stewart 1976; Fig. 11).

Female. — Macropterous. Length of forewings 8-9 mm; length of body 6-9 mm. General body color. and head-pronotal pigmentation similar to male. Subgenital plate truncate posteriorly, lateral margins parallel with sides of abdomen (Szczytko and Stewart 1976; Fig. 12).

Nymph (reared). — Length of mature nymph 8-9 mm. Description essentially the same as for *I. longiseta* (Fig. 5) (see diagnosis under *I. longiseta*).

Ova. — General shape oval, cross section circular (Szczytko and Stewart 1977; Fig. 16). Collar reduced, chorion covered with evenly spaced punctations, ridges reduced, micropyles arranged in pairs or threes near bottom 1/2, on one side.

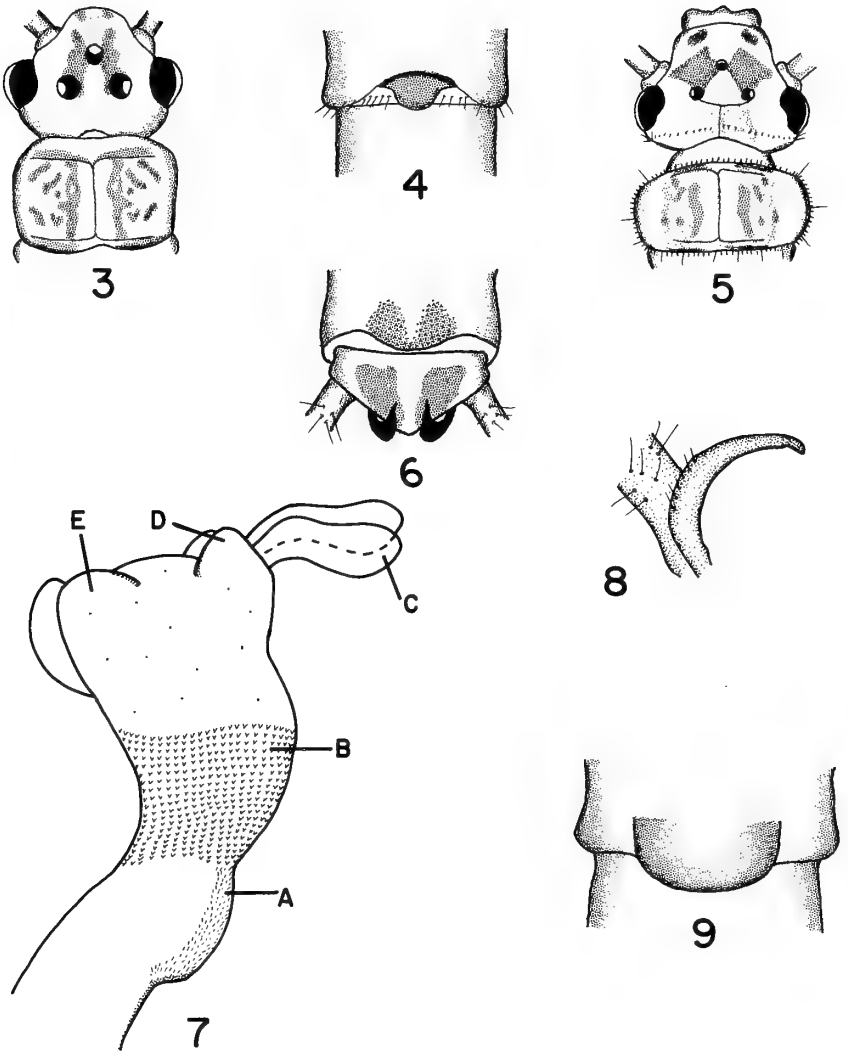
Material examined. — TYPES: Holotype ♂, allotype, and 6 ♂, 17 ♀, and 2 exuvia; paratypes, TEXAS, El Paso Co., 5-10 mi. S. of El Paso, on rd. to Marathon, in *Tamarix* along irrigation ditch, 22/IV/1939, J. A. and H. H. Ross (INHS). Additional specimens — COLORADO: Huerfano Co., La Veta Pass, 21/VII/1938, D. J. and J. N. Knull, 1 ♂ (INHS).

Distribution. — USA: COLORADO and TEXAS (Fig. 2).

Diagnosis and Discussion. — *I. jewetti* is closest to *I. longiseta,* and females and nymphs cannot be separated (see discussion under *I. longiseta*).

This rare species is restricted to Texas and Colorado. Attempts to collect additional specimens from the type locality have been unsuccessful, and the population may now be extinct, due to the heavy use of pesticides in the irrigation ditches and canals in that area (Szczytko and Stewart 1976).

No life history or general biology data is available. Emergence occurs in the middle of Apr. in Texas, and the middle of Jul. in Colorado, based on the specimens examined.



FIGURES 3-9. — *I. longiseta.* 3. adult head and pronotum (scale: 1 mm = .05 mm). 4. male vesicle and 8th sternum (1 mm = .03 mm). 5. nymph head and pronotum (1 mm = .06 mm). 6. male terminalia, dorsal aspect (1 mm = .03 mm). 7. male aedeagus, lateral aspect, A. posteroventral band of small fine hair-like spinulae, B. mesal band of short stout spinulae, C. posterodorsal tubular processes, D. posterodorsal lobes, E. anterodorsal lobes (1 mm = .02 mm). 8. male paraproct, lateral aspect (1 mm = .01 mm). 9. female subgenital plate (1 mm = .03 mm).

Isoperla longiseta Banks

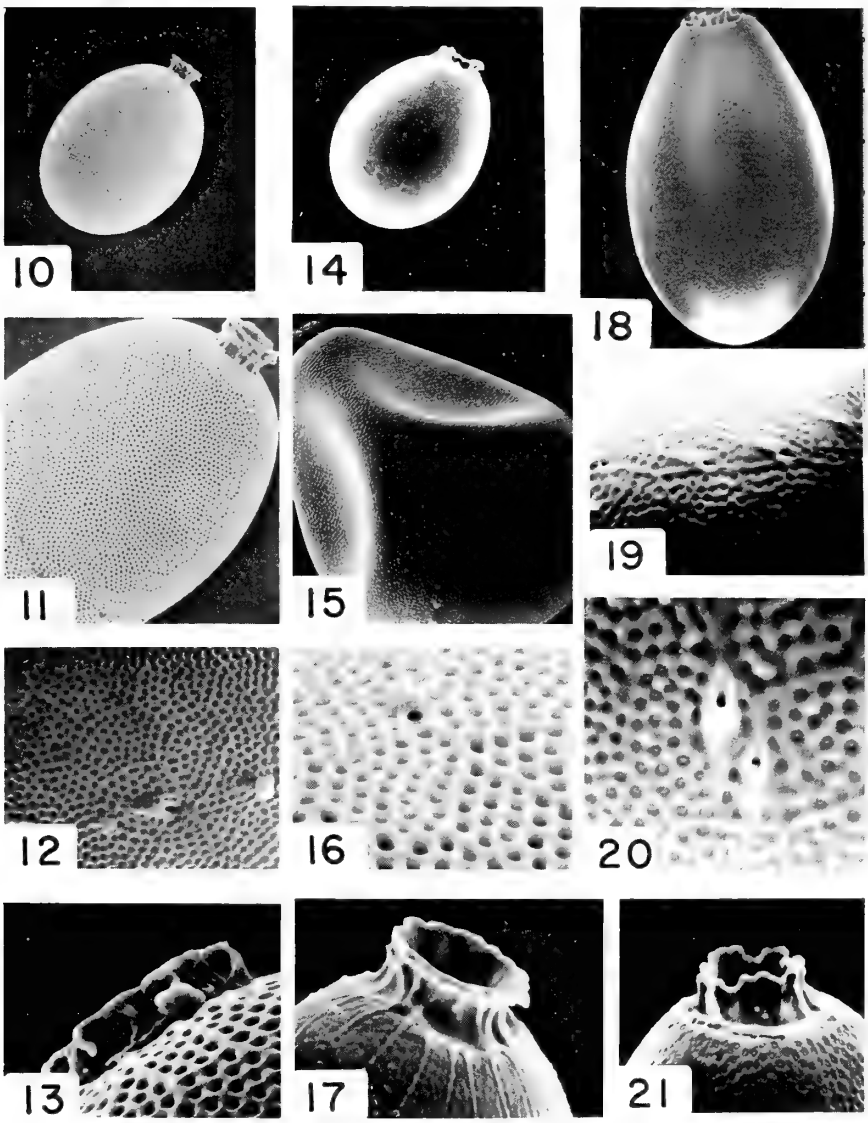
Isoperla longiseta Banks, 1906a, 38:337. Holotype ♀; Onaga Kansas, USA, (MCZ #11,336), (female genitalia).
Isoperla longiseta, Needham and Claassen, 1925, 2:156 (male and female genitalia).
Isoperla longiseta, Claassen, 1940, 232:203.
Isoperla longiseta, Frison, 1942, 21:318. In part.
Isoperla longiseta, Illies, 1966:408.
Isoperla longiseta, Zwick, 1973:247.
Additional references: *Isoperla longiseta,* Banks, 1907; Neave, 1934; Ricker, 1943 (male and female genitalia, female head-pronotal pattern, and forewing), 1946 & 1964; Harden and Mickel, 1952; Gaufin, 1955; Jewett, 1959; (male genitalia) Gaufin et al., 1966 (male and female genitalia), 1972 (male and female genitalia); Knight et al., 1965b (ova); Hitchcock, 1974; Stewart et al., 1974; Ricker and Scudder, 1975; Szczytko and Stewart, 1976 & 1977; Baumann et al., 1977 (male and female genitalia).

Male. — Macropterous. Length of forewings 6-8 mm; length of body 5-7 mm. General body color light yellow to yellowish brown. Lateral ocelli of head connected to anterior ocellus by a dark "H"-shaped pigment pattern. Interocellar space light yellow (Fig. 3). Anterior frons with 2 small pigment spots. Ninth tergum with bipartite patch of stout hair-like setae and dark brown patches void of setae at posterior margin. Vesicle broader at base than apex (Fig. 4). Posterior margin of cercal segments with very long ventral hair, medium length dorsal hair at posterior margin of segments 1-10. Paraprocts slender, tapering apically to sharp points, with small fine hairs posteriorly, and recurving anteriorly, over ca. 1/3 10th tergum (Figs. 6 & 8). Aedeagus entirely membranous bearing broad even mesal band of short stout spinulae (Fig. 7B); its posteroventral margin with band of small fine hair-like spinulae (Fig. 7A), and apex with 2 anterodorsal, 2 posterodorsal rounded lobes and 2 short posterior tubular processes (Fig. 7C-E).

Female. — Macropterous. Length of forewings 8-10 mm; length of body 6-9 mm. General body color, and head-pronotal pigmentation similar to male. Subgenital plate of 8th sternum nearly semicircular, lateral margins parallel with sides of abdomen (Fig. 9).

Nymph (reared). — Length of mature nymph 8-11 mm. Dorsum of head with 2 quadrangular dark areas connecting lateral ocelli with anterior ocellus. Interocellar space light. Faint occipital ridge, with sparse, small spinulae on back of head. Pronotum fringed with short stout hairs; long stout hairs interspersed, except anterior margin (Fig. 5). Abdominal terga with 3 longitudinal stripes, and 8 faint rows of longitudinal dots (sometimes absent), 2 mesal, and 3 lateral. Femora and tibiae with dorsal fringe of long fine hairs, and tarsi with shorter fringe. Posterior margin of cercal segments encircled with small stout hairs; dorsal fringe of short hairs become progressively longer segments 13-17; one long hair both ventrally and dorsally at posterior margin of remaining segments.

Ova. — General shape oval, cross section circular (Fig. 18). Color honey. Length .21 mm, width .13 mm. Collar well developed, with partitioned projections; chorion covered with many evenly spaced punctations (Figs. 18-20), micropyles slightly raised, and arranged in pairs or threes near bottom 1/3, on one side (Figs. 18-20).



FIGURES 10-21. — Figs. 10, 11, 13 & 16. *I. mormona.* 10. whole ova 200×. 11. detail of chorion 400×. 13. detail of collar 1000×. 16. detail of micropyle 2000×: Figs. 12, 14, 15 & 17. *I. quinquepunctata.* 12. detail of micropyle 1000×. 14. whole ova 200×. 15. detail of chorion 400×. 17. detail of collar 1000×: Figs. 18-21. *I. longiseta.* 18. whole ova 400×. 19. detail of micropyles 1000×. 20. detail of micropyles 2000×. 21. detail of collar 1000×.

Magnifications represent original values before reduction of plates.

Material examined. — TYPES: Holotype ♀, Kansas: Onaga, Date ?, Creveceur, (MCZ). Additional specimens: *CANADA:* Saskatchewan, Sutherland, 17/VI/1939, W. E. Ricker, 2 ♂ (WR), N. Saskatchewan, Hwy. 5, 13/VII/1973, D. Smith, 4 ♂, 14 ♀ (US). *USA:* COLORADO: Grand Co., 4 mi. N. of Granby, Hwy. 40, Colorado R., 24/VII/1960, Collector ?, 1 ♀ (UU); Moffat Co., Maybell, Yampa R., 18/VII/1968, B. R. Oblad, 3 ♂, 2 ♀ (RWB), Yampa R., 24/VI/1962, A. R. Gaufin, 1 ♂ (UU), Yampa R., 29/VI/1968, B. R. Oblad, 2 ♂ (UU). ILLINOIS: Union Co., Ana, 6/VI/1951, H. H. Ros and Richards, 2 ♀ (WR). IOWA: Story Co., Ames, 10/VI/1931, P. A. Morre, 3 ♀ (INHS). KANSAS: Leavenworth Co., Lawrence, 26/VI/1919, Collector ?, 1 ♀ (CU). MISSOURI: Cole Co., Jefferson City, Missouri R., 29/V/1937, H. H. Ross, 1 ♂, 1 ♀ (INHS). MONTANA: Carbon Co., Clarks Fork of Yellowstone R., 10 mi. above Yellowstone R., 25/VI/1966, J. R. Grierson, 1 ♀ (UU); Custer Co., Miles City, 26/VII/1915, Collector ?, 1 ♂, 2 ♀ (CU); Dawson Co., Glendive, Yellowstone R., 14/VII/1940, H. H. and J. A. Ross, 3 ♂, 7 ♀ (INHS); Fergus Co., 70 mi. S. E. of Malta, Hwy. 191, Missouri R., 6/VII/1966, J. R. Grierson, 1 ♂, 1 ♀ (SJ); Richland Co., Sidney, Yellowstone R., 2/VII/1975, R. L. Newell, 9 ♂, 10 ♀ (ISU); Roosevelt Co., Wolf Point, Missouri R., 14/VII/1940, H. H. and J. A. Ross, 2 ♂, 9 ♀ (INHS). NEBRASKA: Lincoln Co., Lincoln, 11/VI/1944, Collector ?, 2 ♂ (INHS); Richardson Co., Rulo, Missouri R., 12/VI/1944, Collector ?, 1 ♀ (INHS). NEW MEXICO: Rio Arriba Co., San Juan R., 4/VII/1966, S. L. Jensen, 7 ♂, 4 ♀ (RWB), San Juan R., 7/VIII/1960, Coft, 3 ♂, 4 ♀ (SJ). UTAH: Carbon Co., Desolation Canyon, Green R., 8/X/1975, Winget and Reichert, 1 ♀ (RWB); Grant Co., Dewey, Colorado R., 15/V/1954, A. R. Gaufin, 1 nymph (UU), N.W. of Moab, Colorado R., 26/VI/1943, G. F. Knowlton, 41 ♂, 18 ♀ (INHS); Unitah Co., Bonanza, White R., 25/VII/1975, R. W. Baumann, 2 ♂, 1 ♀ (RWB), below Bonanza, Hwy. 45, White R., 25/V/1977, S. W. Szczytko and K. W. Stewart, 7 nymphs, reared 3 ♂, 1 ♀ (SWS & NTSU); San Juan Co., 5 mi. W. of Bluff, San Juan R., 21/VI/1966, Collector ?, 2 ♂ (UU). SOUTH DAKOTA: Buffalo Co., Buffalo, 19/VI/1925, H. C. Severin, 1 ♂, 1 ♀ (INHS); Yankton Co., Yankton, Missouri R., 19/VI/1925, H. C. Severin, 2 ♀ (INHS). WYOMING: McKenzie Co., Yellowstone R., 4/VII/1975, R. L. Newell, 15 nymphs (ISU); Sheridan Co., Sheridan, 29/VI/1949, D. G. Denning, 1 ♂, 2 ♀ (SJ); Sublette Co., Boulder, Trib. Pine Branch R., 20/VI/1940, H. H. Ross, 1 ♀ (INHS); Sweetwater Co., Green R., 30/VI/1959, A. R. Gaufin, 1 ♂ (UU), Green R., 29/VII/1959, A. R. Gaufin, 1 ♂, 1 ♀ (UU), Green R., 12/VII/1959, A. R. Gaufin, C. Smith and Musser, 1 ♂ (UU), Green R., 11/VI/1959, A. R. Gaufin, 8 ♂, 1 ♀ (UU); Weston Co., Upton, 20/VI/1940, H. H. and J. A. Ross, 2 ♂, 1 ♀ (INHS).

Distribution. — CANADA: Alberta, British Columbia, Manitoba, Quebec, Saskatchewan; USA: Colorado, Idaho, Illinois, Iowa, Kansas, Minnesota, Missouri, Montana, New Mexico, South Dakota, Utah and Wyoming (Fig. 2).

Diagnosis and Discussion. — *I. longiseta* is similar to *I. jewetti.* Males can be distinguished by their longer slender paraprocts, absence of a long single finger process dorsally on the aedeagus, and macropterous wings. We were unable to separate females and nymphs. *I. longiseta* ova

are larger than *I. jewetti*, and their chorionic punctations are shallower (Szczytko and Stewart 1976, 1977).

This species extends further eastward than any other typically western *Isoperla*. Frison (1942) stated that it was associated with the prairie and plains states west of the Mississippi River, and that it was replaced in the Rocky Mountains and West Coast by *I. mormona*. Ricker (1946, 1964) indicated that it was the only typically prairie stonefly species inhabiting large river systems. No life history or biological studies have been done on this species.

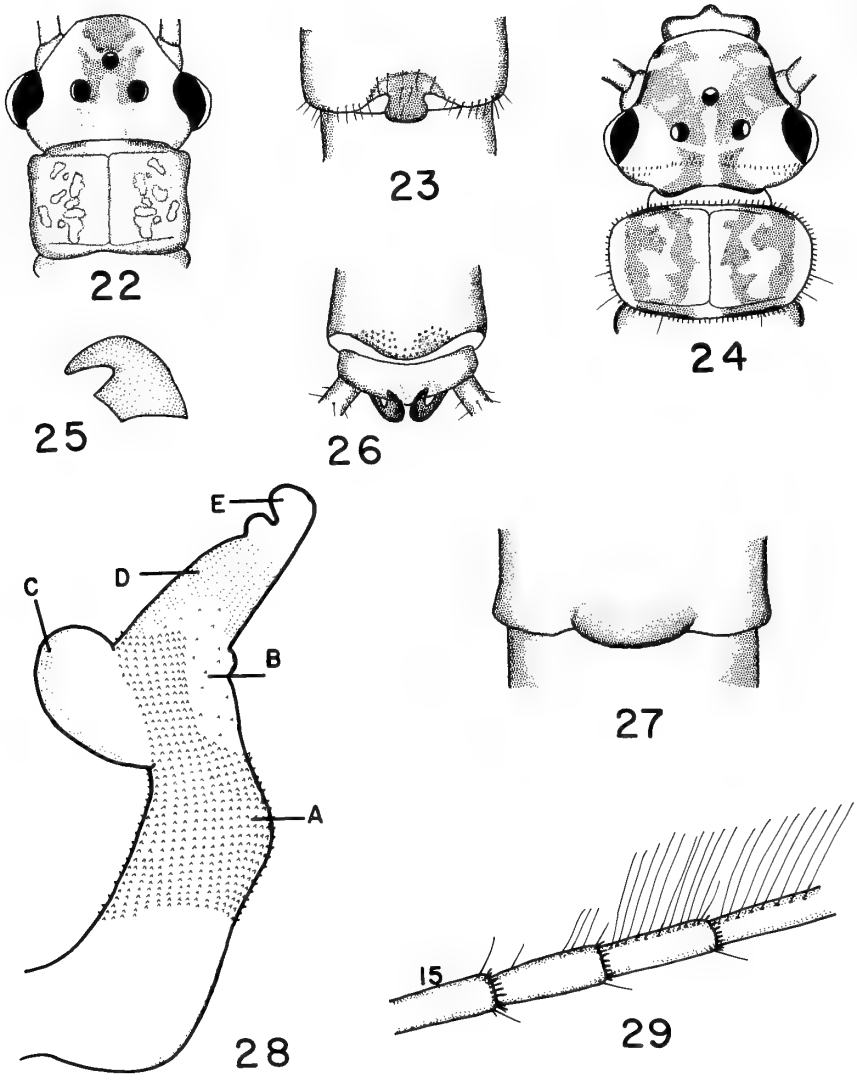
Specimens available indicate that emergence begins during the first week in Jun. and continues until late Aug., with peak emergence occurring late Jun.-Jul.

Isoperla mormona Banks

Isoperla mormona Banks, 1920, 64:322. Holotype ♀; Vinyard Utah, USA, (MCZ #10,822), (female genitalia).
Isoperla marmona, Needham and Claassen, 1925, 2:153.
Isoperla insipida Hoppe, 1938, 4:157. Syn. Frison, 1942.
Isoperla marmona, Claassen, 1940, 232:203.
Isoperla mormona, Frison, 1942, 22:321.
Isoperla mormona, Illies, 1966:410.
Isoperla mormona, Zwick, 1973:247.

Additional references: *Isoperla mormona,* Gaufin, 1955; Jewett, 1959, 1960 (male and female genitalia); Gaufin and Jensen, 1961; Gaufin et al., 1966 (nymphal mesosternum, male and female genitalia); Ricker, 1964; Gaufin, 1964b; Knight et al., 1965b (ova); Logan and Smith, 1966; Knight and Gaufin, 1966, 1967; Newell, 1970; Baumann, 1971; Gaufin et al., 1972 (male and female genitalia); Stewart et al., 1974; Ricker and Scudder, 1975; Baumann et al., 1977 (nymphal mesosternum, male and female genitalia, and habitus).

Male. — Macropterous. Length of forewings 7-9 mm; length of body 6-8 mm. General body color light yellow. Lateral ocelli of head connected to anterior ocellus by "H"-shaped dark brown pigmentation. Interocellar space light yellow. Anterior frons with large median dark brown pigment patch. Pronotum evenly suffused with brown except median light yellow stripe (Fig. 22). Ninth tergum with patch of short stout spinulae (Fig. 26). Posterior margin of cercal segments with long ventral hair, medium length dorsal hair at posterior margin of segments 1-10. Paraprocts short, stout, tapering apically to points and curving outward, recurving anteriorly slightly over 10th tergum (Figs. 25 & 26). Vesicle, truncate posteriorly (sometimes slightly rounded), much darker than rest of segment (Fig. 23). Aedeagus entirely membranous with an irregular large mesal patch of short, stout spinulae (Fig. 28A); anterior margin with a large rounded lobe bearing narrow anterior band of very fine spinulae (Fig. 28C); apical 1/3 tube-like, covered with fine spinulae except at bi-lobed tip (Fig. 28E), posterobasal area of apical tube with scattered patch of short, stout spinulae (Fig. 28B).



FIGURES 22-29. — *I. mormona.* 22. adult head and pronotum (scale: 1 mm = .06 mm). 23. male vesicle and 8th sternum (1 mm = .03 mm). 24. nymph head and pronotum (1 mm = .05 mm). 25. male paraproct, lateral aspect (1 mm = .02 mm). 26. male terminalia, dorsal aspect (1 mm = .04 mm). 27. female subgenital plate (1 mm = .03 mm). 29. nymphal cerci, segs. 15-18 (1 mm = .02 mm). 28. male aedeagus, lateral aspect, A. mesal patch of short stout spinulae, B. scattered patch of short stout spinulae, C. large round anterior lobe, D. patch of small fine spinulae, E. bi-lobed apex (1 mm = .02 mm).

Female. — Macropterous. Length of forewings 8-9 mm; length of body 6-7 mm. General body color, and head-pronotal pigmentation patterns similar to male. Subgenital plate broadly rounded, produced little posteriorly (Fig. 27).

Nymph (Reared). — Length of mature nymph 6-8 mm. Dorsum of head with 2 bands of dark brown pigmentation extending from posterior margin to above occipital ridge, interrupted behind lateral ocelli then continuing to base of antennae and ending as 2 light patches encircled by pigment on anterior frons, 2 light yellow spots within dark pigment lateral to anterior ocellus, narrow light band in interocellar space. Faint occipital ridge, with sparse, small spinulae on back of head (Fig. 24). Pronotum fringed with evenly spaced small stout hairs; long stout hairs irregularly interspersed at posterior angles and margin (Fig. 24). Abdominal terga with 3 longitudinal stripes, 2 lateral and one mesal and 8 faint rows of longitudinal dots, 2 mesal and 3 each laterally. Femora, tibiae, and tarsi with dorsal fringe of long fine hairs; tibia with row of short, stout spines on dorsal margin, and femur with sparse row on ventral margin. Posterior margin of cercal segments encircled by whorl of small stout hairs; medium length hairs both dorsal and ventral at posterior margin after segment 3; incomplete dorsal fringe of medium length hairs on segment 16; continual dorsal fringe of long fine hairs on 17th and remaining segments (Fig. 29).

Ova. — General shape elliptical, cross section circular (Fig. 10). Color light brown. Length .25 mm, width .18 mm. Collar well developed, raised .02 mm from chorion, and expanded at apex (Figs. 10 & 11). Chorion covered with numerous evenly spaced punctations, ridges slightly raised on surface (Figs. 11 & 16). Micropyles arranged in pairs near bottom 1/3, on one side (Figs. 11 & 16).

Material examined. — TYPES: Holotype ♀, UTAH Vinyard, 22/VI/?, Collector ?, #10,822 (MCZ); *I. insipida* Hoppe, Paratypes, WASHINGTON, Cowlitz Co., Castle Rock, 10/VII/1932, G. N. Hoppe, 1 ♂, 1 ♀ (INHS); Kittitas Co., Cle Ellum, 3/VII/1931, G. N. Hoppe, 1 ♂ (INHS). Additional specimens — *USA:* ARIZONA: Apache Co., near Greer, Hwy. 373, Hall Crk., 19/VII/1968, R. W. Baumann, 1 ♀ (RWB), N. Fork White R., 27/VII/1966, R. K. Allen, 2 ♂, 2 ♀ (INHS), near Alchesay National Fish Hatchery, 17/V/1964, S. G. Jewett, 3 ♂, 2 ♀ (SJ); Coconino Co., Oak Crk. Indian Garden, 19/VI/1937, L. K. Gloyd, 3 ♂, 4 ♀ (INHS). CALIFORNIA: Los Angeles Co., Lake Elizabeth Canyon, 26/IV/1950, Collector ?, 5 ♂, 5 ♀ (LCMNH); Siskiyou Co., near Weed, unknown Crk., 10/VII/1975, D. G. Denning, 4 ♂, 1 ♀ (RWB). COLORADO: Archuleta Co., Piedra R., 7/VII/1960, A. R. Gaufin, 13 ♂, 15 ♀ (RWB), Piedra R., 23/VII/1960, L. D. Jensen, 1 ♂, 1 ♀ (RWB), 2 mi. N. of Arboles, Piedra R., 14/VII/1960, A. R. Gaufin, 50 nymphs (UU), Los Pinos R., 8/VII/1960, A. R. Gaufin, 3 nymphs (UU); La Plata Co., Ignacio, Los Pinos R., 7/VIII/1964, A. R. Gaufin, 10 ♂, 12 ♀ (RWB); Montrose Co., 3 mi. N. of Montrose, Uncompahgre R., 15/VII/1962, Collector ?, 3 ♂, 6 ♀ (UU); Park Co., Lake George, S. Platte R., 8/VIII/1943, J. A. and H. H. Ross, 1 ♀ (INHS), Tarryall, Tarryall R., 15/VII/1956, H. H. Ross, 3 ♂, 2 ♀ (SJ); Rio Blanco Co., Meeker, White R., 31/VII/1960, A. R. Gaufin, 10 ♂, 8 ♀ (UU), White R., 13/VII/1961, A. R. Gaufin, 72 ♂, 26 ♀ (UU & BS). IDAHO: Ada Co., Braves Ball Park, Boise R., 15/VIII/1963, S. L. Jensen, 1 nymph (UU); Bonneville Co., Idaho Falls, Snake R., 13/VII/1948, D. R. Merkley, 1 ♂, 3 ♀ (RWB), Hwy. 26, Rainey Cr., 21/VI/1964, S. L. Jensen, 2 nymphs (UU); Fremont Co., Hwy. 32, Fall R., 8/VII/1972, R. L. Newell, 1 ♀ (ISU), Hwy. 191, Buffalo R., 23/VI/1964, S. L. Jensen, 8 nymphs (UU); Power

Co., 10 mi. W. of Pocatello, Hwy. 30, Banncok Crk., 20/VI/1964, J. W. Richardson and S. L. Jensen, 2 ♂, 3 ♀ (UU). MONTANA: Beaverhead Co., 15 mi. S. of Dillon, Beaverhead R., 19/VI/1965, A. V. Nebeker, 3 ♂ (UU), 5 mi. N.E. of Dillon, Beaverhead R., 5-6/VII/1966, J. R. Grierson, 1 ♂, 4 ♀ (UU), 24 mi. N. of Dillon, Big Hole R., 5/VIII/1966, J. R. Grierson, 1 ♂, 1 ♀ (UU), Broadwater Co., Toston, Missouri R., 22/VI/1940, J. A. and H. H. Ross, 3 ♂, 7 ♀ (INHS); Cascade Co., Great Falls, Missouri R., 24/VI/1965, A. V. Nebeker, 1 ♂ (UU); Fergus Co., 2.2 mi. S.E. of Lewistown, Spring Crk., 5/VI/1966, J. R. Grierson, 1 ♂, 2 ♀ (UU); Glacier Co., Glacier National Park, St. Mary's Campground, St. Mary's R., 10/VII/1964, A. R. Gaufin, 1 ♀ (UU); Granite Co., near Phillipsburg, Flint Crk., 6/VIII/1965, A. R. Gaufin, 10 ♂, 13 ♀ (UU); Jefferson Co., 15 mi. S.E. of Helena, Boulder R., 14/VIII/1966, J. R. Grierson, 1 ♂, 5 ♀ (UU); Madison Co., 2 mi. above Ruby Dam, Ruby R., 6/VIII/1966, J. R. Grierson, 1 ♀ (UU); Pondera Co., Dupuyer, Dupuyer Crk., 26/VII/1967, A. R. Gaufin, 12 ♂ (UU). NEW MEXICO: Catron Co., Apache National Forest, Cottonwood Campground, 13/VII/1967, R. and D. Koss, 3 ♂ (RWB), Gila National Monument, W. Fork Gila R., 17/V/1974, M. and E. Cather, 3 ♂, 2 ♀ (BS); Grant Co., E. Fork Gila R., N. of Junct. with W. Fork, 16/V/1976, W. L. Minckley and D. Bruns, 7 ♂, 5 ♀ (WR), Hwy. 15, Gila R., 17/V/1974, M. and E. Cather, 16 ♂, 12 ♀, 3 nymphs (BS); Lincoln Co., 1/2 mi. above Bonito Lake, Rio Bonito R., 19/VI/1965, R. W. Baumann, 2 ♂, 2 ♀, 14 nymphs (RWB); Rio Arriba Co., San Juan R., 7/VIII/1960, Collector ?, 7 ♂, 5 ♀ (SJ). OREGON: Benton Co., 9 mi. N. of Corvallis, Berry Crk., 30/VII/1960, Collector ?, 2 ♂, 2 ♀ (SJ), Corvallis, Oak Crk., 21/IV/1935, W. M. W., 1 ♀ (INHS); Clackamas Co., Molalla, Molalla R., 1/VII/1935, S. G. Jewett, 1 ♀ (INHS); Deschutes Co., Lapine, Little Deschutes R., 13/VII/1948, S. G. Jewett, 3 ♂, 2 ♀ (LCMNH); Harney Co., Frenchglen, Blitzen R., 11/VII/1935, S. G. Jewett, 6 ♂, 3 ♀ (LCMNH); Klamath Co., 12 mi. E. of Chiloquin, Sprague R., 1-3/VII/1951, B. Malin, 6 ♂, 4 ♀ (UU), Crooked Crk., 8/VII/1940, F. Glover, 4 ♂, 4 ♀ (RWB), Klamath Falls, ?/VII/1953, J. Schuh, 1 ♂ (OSU[2]); Malheur Co., Trout Crk., 30/VII/1937, S. G. Jewett, 3 ♂, 1 ♀ (INHS). UTAH: Carbon Co., Spring Glen, Provo R., 19/VII/1952, A. R. Gaufin, 9 ♂, 8 ♀ (UU); Duchesne Co., Duchesne, Duchesne R., 3/VIII/1973, B. P. Stark and R. W. Baumann, 2 ♂, 3 ♀ (BS); Morgan Co., Henifer, 15/VIII/1943, G. F. Knowlton and Maddock, 1 ♂ (INHS); Piute Co., Hwy. 89, N. of Big Rock Candy Mt., Sevier R., 2/VI/1977, S. W. Szczytko and K. W. Stewart, 40 nymphs (reared 8 ♂, 7 ♀), (SWS and NTSU); Sevier Co., Big Rock Candy Mt., Sevier R., 15/VII/1963, G. F. Knowlton, 1 ♂, 2 ♀ (UU), Big Rock Candy Mt., Sevier R., 13/VII/1961, G. F. Knowlton, 1 ♂, 5 ♀ (UU), Elsinore, 22/VII/1937, G. F. Knowlton, 2 ♀ (INHS), Summit Co., 1 mi. W. of Peoa, Weber R., 28/VII/1973, B. P. Stark, 2 ♂ (BS); Unitah Co., Hwy. 45, below Bonanza, 25/V/1977, S. W. Szczytko and K. W. Stewart, 11 nymphs (reared 2 ♂, 6 ♀), (SWS and NTSU), 4 1/2 mi. N. of Whiterock, Whiterock R., 6/VIII/1975, Collector ?, 1 ♀ (RWB); Wasatch Co., Heber, 14/VIII/1943, G. F. Knowlton and Maddock, 1 ♀ (INHS), Charleston, 14/VIII/1943, G. F. Knowlton and Maddock, 1 ♀ (INHS), Snake Crk., 7/VIII/1975, Sakamoto, 1 ♂ (RWB), Hwy. 40, Provo R., 20/VII/1972, B. P. Stark, 2 ♂ (BS); Weber Co., Ogden, 12-14/VII/1960, G. F. Knowlton, 1 ♂, 5 ♀ (UU), Ogden, 13&17/VII/1959, G. F. Knowlton, 11 ♀ (UU). WYOMING: Carbon Co., Riverside, Yellowstone National Park, Madison R., 26/VI/1964, Heaton, 7 ♂, 11 ♀ (RWB), Madison R., 2/V/1964, Heaton, 30 nymphs (UU);

Lincoln Co., La Barge, Green R., 17/VII/1962, A. V. Nebeker, 1 ♂, 1 ♀, (SJ); Sublette Co., Daniel, Hwy. 189, Horse Crk., 18/VII/1962, Collector ?, 3 ♂, 3 ♀ (UU), N.W. of Daniel Hwy. 187, Green R., 19/VII/1962, Collector ?, 1 ♂, 1 ♀ (UU), N. of Cora, Willow Crk. 18/VII/ , Collector ?, 1 ♀ (UU), Daniel, Hwy. 189, Prairie Crk., 18/VII/1962, Collector ?, 2 ♂, 1 ♀ (UU), Big Pine, Hwy. 189, S. Piney Crk., 18/VII/1962, Collector ?, 4 ♂, 3 ♀ (UU); Teton Co., 1 mi. S. of entrance to Yellowstone National Park, Pole Cat Crk., 27/VI/1964, J. W. Richardson and S. L. Jensen, 4 ♂, 3 ♀ (RWB), Hwy. 26, Gros Ventre R., 23/VI/1964, J. W. Richardson and S. L. Jensen, 2 nymphs (UU).

Distribution. — CANADA: British Columbia; USA: Arizona, California, Colorado, Idaho, Montana, New Mexico, Oregon, Utah, Washington, Wyoming (Fig. 2).

Diagnosis and Discussion. — *I. mormona* is similar to *I. longiseta.* Males can be distinguished by their shorter stouter paraprocts, aedeagus with tubular apex and expanded lobe, truncate vesicle, spinulae pattern of the 9th tergum, distinct "H" pigment pattern and anterior dark patch on head, and by the evenly suffused brown pigmentation of the pronotum. Females can be distinguished by the shallow subgenital plate, and pigmentation patterns described above. Nymphs can be separated by the darker pigmentation of the head and pronotum, long hairs only at lower angles and posterior margin of the pronotum, longer dorsal fringe of hairs on the tarsus, and by the continuous dorsal fringe of long hairs on the cerci after the 16th segment. Ova can be distinguished by the deeper chorionic punctations, slightly raised ridges, and the non-elevated micropyles.

Knight and Gaufin (1966) reported that *I. mormona* was a stenothermic stonefly limited to low altitudes. No studies on the life history or biology have been done on this species. Material examined indicates that emergence begins about the middle of May in southern latitudes and continues until mid-Aug., with peak emergence probably occurring mid-Jul.

Isoperla quinquepunctata (Banks)

Chloroperla quinquepunctata Banks, 1902, 34:124. Holotype ♀; Gallinas R., Las Vegas, New Mexico, USA, (MCZ #11,337).
Isoperla quinquepunctata, Banks, 1906b, 17:175.
Isoperla quinquepunctata, Banks, 1907a:13.
Isoperla quinquepunctata, Claassen, 1940, 232-204.
Isoperla patricia Frison, 1942:313. Holotype ♂, and allotype, Spearfish, Spearfish R., Lawerence Co., South Dakota, (INHS).
NEW SYNONYMY:
Perliola quinquepunctata, Banks, 1947, 54:284.
Isoperla patricia, Illies, 1966:415.
Isoperla quinquepunctata, Illies, 1966:416.

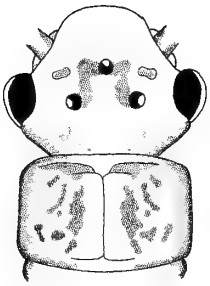
Isoperla patricia, Zwick, 1973:249.
Isoperla quinquepunctata, Zwick, 1973:250.

Additional references: *Isoperla quinquepunctata,* Seemann, 1927 (nymphal description, no illustrations); Needham and Claassen, 1925 (male and female genitalia); Dodds and Hisaw, 1925; Muttkowski, 1929, Claassen, 1931 (nymphal description, no illustrations); Banks, 1947 (wing, adult maxillary palpus, and ocellar area); Gaufin, 1955; Jewett, 1960; Gaufin et al., 1966 (male and female genitalia); Stewart et al., 1974; Baumann et al., 1977 (male and female genitalia). *Isoperla patricia,* Frison, 1942 (adult head and pronotum, male and female genitalia, aedeagus, nymphal mandibles, maxillae, labium, and habitus); Ricker, 1943, 1946; Gaufin, 1955; Jewett, 1959, 1960 (nymphal labium, male and female genitalia); Gaufin and Jensen, 1961; Gaufin, 1964b; Knight et al., 1965a (ova); Nebeker and Gaufin, 1966a; Gaufin et al., 1966 (male and female genitalia); Gaufin et al., 1972 (male and female genitalia); Stewart et al., 1974; Ricker and Scudder, 1975; Baumann et al., 1977 (male and female genitalia).

Male. — Macropterous-brachypterous. Length of forewings (macropterous) 7-9 mm; length of body 8-10 mm; length of forewings (brachypterous) 3-4 mm; length of body 8-10 mm. General body color light brown, often with reddish brown abdomen. Meso- and metathorax dark brown at posterior half. Lateral ocelli connected to anterior ocellus by "r-shaped" band of dark brown pigmentation; 2 dark spots lateral to anterior ocellus. Interocellar area light yellow. Pronotum with dark brown rugosities, and median light yellow stripe (Fig. 30). Ninth and 10th terga with median light furrow, and bipartite patches of long hair-like setae (area of patches sometimes reduced or absent), (Fig. 31). Abdominal terga with patches of long stout hairs at lateral posterior margins. Paraprocts long, curving inward, meeting medially, tapering apically to points and recurving anteriorly over 1/4 10th tergum (Figs. 31 & 34). Vesicle, rounded posteriorly, broader at base than apex (Fig. 35) (sometimes constricted at middle, Fig. 33), base with narrow band of dark pigmentation (Figs. 33 & 35). Aedeagus entirely membranous with 2 mesal, anterolateral lobes covered with small fine spinulae (Fig. 36B) and small posterior lobe with membranous tip void of spinulae (Fig. 36D), apex wider, truncate, void of spinulae and bearing posterior pointed conical lobe (Fig. 36E), heavy band of short, stout spinulae encircling aedeagus above mesal lobes (Fig. 36C), band of finer spinulae encircling aedeagus mesally (Fig. 36B); ventral posterior margin with short band of stout spinulae (Fig. 36A).

Female. — Macropterous. Length of forewings 9-11 mm; length of body 9-11 mm. General body color, and head-pronotal pigmentation patterns similar to male. Subgenital plate variable (see Frison, 1942:313), but generally triangular, produced

FIGURES 30-37. — *I. quinquepunctata.* 30. adult head and pronotum (scale: 1 mm = .08 mm). 31. male terminalia, dorsal aspect (1 mm = .04 mm). 32 nymph head and pronotum (1 mm = .09 mm). 33. male vesicle and 8th sternum (1 mm = .04 mm). 34. male paraproct, lateral aspect (1 mm = .02 mm). 35. male vesicle variation (1 mm = .04 mm). 36. male aedeagus, lateral aspect, A. posteroventral band of stout spinulae, B. mesolateral lobe bearing scattered fine spinulae, C. dense band of short stout spinulae, D. small posterior lobe devoid of spinulae, E. posterior conical lobe (1 mm = .02 mm). 37. female subgenital plate (1 mm = .04 mm).



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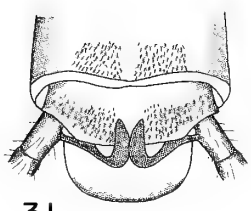

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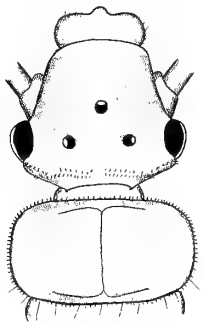

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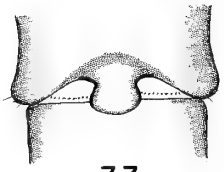

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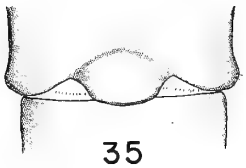

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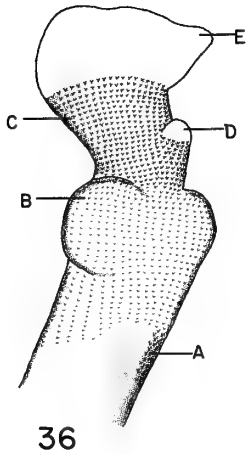

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posteriorly 1/4 the length of 9th sternum, notched at apex, and darker than rest of segment (Fig. 37).

Nymph (Reared). — Length of mature nymph 9-13 mm. Dorsum of head with light brown, quadrangular areas connecting lateral ocelli with anterior ocellus, 1 light spot between base of each lateral ocellus and posterior margin. Interocellar area light with narrow band extending back to occiput. Faint occipital ridge, with sparse, small spinulae on back of head (Fig. 32). Pronotum fringed with evenly spaced small stout hairs; long hairs interspersed at posterior angles and margin; dorsum mostly light except for 2 light lateral brown bands, rugosites absent (Fig. 32). Abdominal terga with 3 longitudinal stripes, 2 lateral and 1 mesal. Femora and tibiae with heavy fringe of long dorsal hairs, tarsi with sparse row of long fine hairs. Posterior margin of cercal segments encircled by whorl of small stout hairs; incomplete dorsal fringe of long fine hairs on segment 16; continual dorsal fringe on 17th and remaining segments.

Ova. — General shape oval, cross section of anterior 1/2 triangular, cross section posterior 1/2 round (Fig. 15). Color medium brown. Length .24 mm; width .19 mm. Collar well developed, raised .02 mm from chorion (Figs. 14 & 17). Chorion covered with numerous evenly spaced punctations, ridges produced slightly (Figs. 12 & 15). Micropyles arranged in threes near bottom 1/3, on one side (Figs. 12 & 14).

Material examined. — TYPES: *I. quinquepunctata,* Holotype ♀, NEW MEXICO: San Miguel Co., Las Vegas, Gallinas R., 9/VI/?, Cockerell, #11,337 (MCZ). Paratypes, *I. patricia;* UTAH: Cache Co., Paradise, 14/VI/1938, Hardy and Stains, 1 ♂, 11 ♀ (INHS), Logan Canyon, 11/VII/1938, D. E. and A. T. Hardy, 1 ♀ (INHS). Additional specimens — *CANADA* — BRITISH COLUMBIA: Prince George, Nechako R., 13-15/VII/1938, W. E. Ricker, 1 ♂, 1 ♀, 1 nymph (INHS). *USA* — CALIFORNIA: Mono Co., near Crestview, Big Spring, 17/VI/1960, S. G. Jewett, 9 ♂, 8 ♀ (SJ); Tehama Co., near Red Bluff, Sacremento R., 31/VII/1965, S. G. Jewett, 3 ♂ (USNM), near Red Bluff, Sacremento R., 12/IV/1960, S. G. Jewett, 1 ♂, 2 ♀, and exuvia (SJ). COLORADO: Archuletta Co., Piedra R., 8/VII/1960, A. R. Gaufin, 4 ♂, 2 ♀, 6 nymphs (RWB); Boulder Co., near Boulder, St. Uroin R., 24/VII/1960, A. R. Gaufin, 12 ♂, 15 ♀ (UU); Conejos Co., 3 mi. S. of La Manga Pass, Hwy. 17, Los Pinos R., 7/V/1976, S. W. Szczytko and K. W. Stewart, 5 ♂, 10 nymphs (SWS & NTSU), 3 mi. E. of La Manga Pass, Correjos R., 7/V/1976, S. W. Szczytko and K. W. Stewart, 3 ♂ (SWS & NTSU); Douglas Co., West Crk., 11/VIII/1958, 1 ♂, 1 ♀, J. A. and H. H. Ross (RWB); Eagle Co., 42 mi. E. of Glenwood Springs, Eagle R., 10/V/1976, S. W. Szczytko and K. W. Stewart, 3 ♂ (SWS & NTSU); Fremont Co., 2 mi. W. of Coaldale, Arkansas R., 30/VI/1974, S. J. Herman, 2 ♂, 1 ♀ (RWB); Garfield Co., Glenwood Springs, Roaring Fork R., 13/VII/1961, A. R. Gaufin, 22 ♂, 17 ♀ (UU); Grand Co., 3 mi. W. of Granby, Colorado R., 20/VI/1961, A. R. Gaufin, 50 nymphs (UU), W. of Granby, Hwy. 40, Colorado R., 27/VI/1962, A. R. Gaufin, 1 ♀ (UU), 4 mi. W. of Granby, Colorado R., 24/VIII/1960, A. R. Gaufin, 10 ♂, 8 ♀ (UU), W. of Granby, Hwy. 40, Colorado R., 27/VI/1962, A. R. Gaufin, 10 ♀ (UU); Granite Co., Hwy. 50, Arkansas R., 12/VII/1961, Collector ?, 18 ♂, 20 ♀ (UU), Arkansas R., 12/VII/1961, Collector ?, 1 ♂ (UU); Gunnison Co., above Hwy. 50, Soap Crk., 1/VII/1962, A. R. Gaufin, 12 ♂, 15 ♀ (UU), Gunnison R. at junct. with Beaver Crk., 7/VI/1961, Collector ?, 8 nymphs (UU), Cebolla Crk. at Powderhorn bridge, 18/VI/1962, Collector ?, 15 nymphs (UU), Beaver Crk. above junct. with

Gunnison R., 4/VII/1964, Collector ?, 5 nymphs (UU), Soap Crk. at junct. with Gunnison R., 1/VII/1961, Collector ?, 3 ♂, 1 ♀ (UU), Soap Crk. at junct. with Gunnison R., 19/IV/1962, A. R. Gaufin, 25 nymphs (UU), W. Elk Crk., 3/VII/1961, A. R. Gaufin, 15 nymphs (UU), below Sargents, Hwy. 50, Tomichi Crk., 12/VII/1962, A. R. Gaufin, 10 nymphs (UU), Hwy. 114, Cochetopa Crk., 12/VII/1962, A. R. Gaufin, 1 ♂, 1 ♀, 15 nymphs (UU), W. Elk Crk. at junct. with Gunnison R., 3/VII/1961, Collector ?, 3 ♀ (UU); Huerfano Co., 2 mi. E. of La Veta Pass, Hwy. 160, 6/V/1976, S. W. Szczytko and K. W. Stewart, 3 ♂, 2 ♀, 2 nymphs (SWS & NTSU), 1 mi. W. of La Veta Pass, Hwy. 160, 6/V/1976, S. W. Szczytko and K. W. Stewart, 2 ♂, 1 ♀, 3 nymphs (SWS & NTSU); Jackson Co., S.W. of Walden, Hwy. 14, Grizzly Crk., 9/V/1976, S. W. Szczytko and K. W. Stewart, 2 ♂, 1 ♀ (SWS & NTSU); Mesa Co., Grand Junction, Colorado R., 1/VI/1961, A. R. Gaufin, 2 nymphs (UU), 2 mi. S.E. of De Beque, Colorado R., 11/VIII/1973, B. P. Stark and R. W. Baumann, 1 ♀ (BS); Moffat Co., Dinosaur National Monument, Pool Crk., 25/VII/1962, D. W. Anderson, 3 nymphs (UU), 4 mi. S.W. of Craig, Hwy. 13, Yampa R., 3/VII/1974, B. P. Stark, 6 ♂, 2 ♀ (BS); Montezuma Co., Mancos, Chicken Crk., 8/VII/1960, A. R. Gaufin, 1 ♂, 1 ♀ (RWB); Montrose Co., Hwy. 50, Cimarron Crk., 20/IV/1962, A. R. Gaufin, 6 nymphs (UU), 13 mi. above Montrose, Uncompahgre R., 14/VII/1962, A. R. Gaufin, 1 ♂ (UU); Ouray Co., Hwy. 550, Cow Crk., 15/VII/1962, A. R. Gaufin, 2 nymphs (UU); Park Co., Hartzel, S. Platte R., 18/VIII/1938, J. A. and H. H. Ross, 3 ♂, 1 ♀ (INHS); Pitkin Co., S. of Carbondale, Hwy. 133, Crystal R., 10/V/1976, S. W. Szczytko and K. W. Stewart, 3 nymphs (SWS & NTSU); Rio Blanco Co., 2 mi. N. of Meeker, White R., 22/VI/1961, Collector ?, 8 nymphs (UU), Hwy. 5, Piceance Crk., 25/V/1977, S. W. Szczytko and K. W. Stewart, 25 nymphs (reared 8 ♂, 4 ♀), (SWS & NTSU), 2 mi. N. of Meeker, White R., 22/VI/1961, A. R. Gaufin, 2 ♀ (UU), Piceance Crk., 15/VI/1976, L. Grey, 15 ♂, 11 ♀, 8 nymphs (CSU); Routt Co., Hideaway, Yampa R., 29/VI/1968, B. R. Oblad, 6 ♂, 3 ♀ (RWB), Soda Crk., 16/VII/1968, B. R. Oblad, 1 ♂ (UU), E. Fork Elk R., 18/VII/1968, B. R. Oblad, 3 ♂, 1 ♀ (UU), Yampa R., 15/VII/1968, B. R. Oblad, 10 ♂, 20 ♀ (UU), Steamboat Springs, Yampa R., 25/VI/1962, A. R. Gaufin, 5 ♂, 6 ♀ (UU), Yampa R., 16/VII/1968, B. R. Oblad, 28 ♀ (UU), Focus Ranch, Little Snake R., 17/VII/1968, B. R. Oblad, 2 ♂, 1 ♀ (UU), 1 mi. W. of Hayden, Yampa R., 18/VII/1968, B. R. Oblad, 2 ♂, 11 ♀ (UU); Saquache Co., Sargents, Tomichi Crk., 11/VII/1961, A. R. Gaufin, 10 nymphs (UU); San Juan Co., Silverton, ?/VII/?, Oslay, 1 ♂ (CU); San Miguel Co., 3 mi. N. of Placerville, Hwy. 62, Leporad Crk., 11/V/1976, S. W. Szczytko and K. W. Stewart, 8 ♂, 3 ♀ (SWS & NTSU). IDAHO: Bear Lake Co., 1/2 mi. N. of Geneva, Hwy. 89, Thomas Fork Crk., 29/VI/1964, J. W. Richardson and S. L. Jensen, 4 ♂, 6 ♀, 3 nymphs (UU); Custer Co., N. of Challis, Salmon R., 19/VI/1963, A. R. Gaufin, 3 ♂, 9 ♀ (RWB); Franklin Co., 4 mi. N. of Preston, Hwy. 34, Bear R., 20/VI/1964, J. W. Richardson and S. L. Jensen, 3 ♂, 9 ♀ (UU), near Preston, Glendale Reservoir, 24/IV/1952, Collector ?, 1 nymph (UU); Fremont Co., 5 mi. S. of Island Park Reservoir, Henry's Fork, Snake R., 23/VI/1964, J. W. Richardson and S. L. Jensen, 3 ♂, 5 ♀ (UU), St. Anthony, Henry's Fork of Snake R., 19/VI/1955, S. G. Jewett, 1 ♂, 1 ♀ (UU), 2 mi. N. of Ashton, Hwy. 191, Warm R., 23/VI/1964, J. W. Richardson and S. L. Jensen, 4 nymphs (UU), Mack's Inn, Hwy. 191, Henry's Fork of Snake R., 24/VI/1964, J. W. Richardson and S. L. Jensen, 74 nymphs (UU); Jefferson Co., 1 mi. E. of Ririe, Hwy. 26, Birch Crk., 21/VI/1964, J. W. Richardson

and S. L. Jensen, 2 nymphs (UU); Lemhi Co., N. Fork Salmon R., 16/VI/1965, A. R. Gaufin, 47 ♂, 60 ♀ (UU), S. of North Fork, Hwy. 93, Wagonhammer Spring, 17/VI/1965, A. R. Gaufin, 1 ♀ (UU), Ellis, Salmon R., 17/VIII/1963, A. R. Gaufin, 1 ♂ (UU), N. of Salmon, Salmon R., 19/VI/1963, A. R. Gaufin, 1 ♀ (UU), 8 mi. S.W. of Shoup, Garden Crk., 4-6/VII/1969, C. R. Whitt, 1 ♀ (UU). MONTANA: Beaverhead Co., 5 mi. N.E. of Dillon, Beaverhead R., 6/VIII/1966, J. R. Grierson, 1 ♂, 1 ♀ (UU); Big Horn Co., 3 mi. W. of Wyola, Big Horn R., 22/VII/1966, J. R. Grierson, 2 ♂ (UU); Broadwater Co., Toston, Missouri R., 22/VI/1940, J. A. and H. H. Ross, 1 ♀ (INHS); Carbon Co., Barron Crk., 19/VI/1969, T. Dodson, 2 ♂, 2 ♀ (UU), 10 mi. above Yellowstone R., Clark's Fork of Yellowstone R., 25/VI/1966, J. R. Grierson, 4 ♂, 6 ♀ (UU); Cascade Co., at Sun R., Hwy. 20, Sun R., 24/VI/1965, A. V. Nebeker, 1 ♂ (UU); Fergus Co., 2 mi. E. of Lewistown, Spring Crk., 5/VII/1966, J. R. Grierson, 11 ♂, 13 ♀ (UU); Flathead Co., Glacier National Park, Bowman Crk., 24/VII/1970, A. R. Gaufin, 15 ♂, 10 ♀ (UU), Glacier National Park, N. Fork Flathead R., 14/VII/1967, A. R. Gaufin, 3 ♂, 11 ♀ (UU); Glacier National Park, Kintla Crk., 23/VII/1970, A. R. Gaufin, 6 ♀ (UU); Glacier Co., Glen's Lake, Crk. at outlet, 4/VII/1970, C. Yarmoloy, 2 ♀ (UU), Glacier National Park, Swift Current Lake, 11/VII/1964, A. R. Gaufin, 2 ♂ (UU), Glacier National Park, St. Mary's Campground, St. Mary's R., 10/VII/1964, A. R. Gaufin, 2 ♂, 2 ♀ (UU); Gallatin Co., W. Gallatin R., 9/VIII/1951, R. Hays, 3 ♂, 1 ♀ (CU); Judith Basin Co., 13 mi. N.E. of Geyser, Arrow Crk., 7/VII/1966, J. R. Grierson, 1 ♀ (UU); Lake Co., Condon, Swan R., 28/VI/1969, P. Milam, 6 ♂, 7 ♀ (UU); Lincoln Co., Hwy. 37, Kootenai R., 4/VII/1968, 40 ♂, 38 ♀ (UU); Meagher Co., Martinsdale, S. Fork of Mussel Shell R., 1/VII/1966, J. R. Grierson, 2 ♂, 1 ♀ (UU), Cottonwood Crk., 1/VII/1966, J. R. Grierson, 1 ♀ (UU); Missoula Co., Alva Lake outlet, Clearwater R., 20/VI/1969, R. L. Newell, 10 ♀ (UU), Hwy. 20, Blackfoot R., 8/VII/1964, A. R. Gaufin, 10 ♂, 18 ♀ (UU), 16 mi. above Hwy. 93, Lolo R., 16/VII/1965, J. R. Grierson, 1 ♂ (UU), Swan Valley, Hwy. 209, Morrel Crk., 8/VII/1964, A. R. Gaufin, 1 ♂ (UU); Park Co., 7 mi. above Yellowstone R., Shields R., 1/VII/1966, J. R. Grierson, 3 ♂, 5 ♀ (UU), Livingston, Yellowstone R., 3/VII/1938, Forsyth and Platsch, 1 ♀ (UU); Ravalli Co., N. of Hamilton, Hwy. 93, Bitterroot R., 23/VII/1965, J. R. Grierson, 3 ♂, 4 ♀ (UU), Ravalli, Hwy. 93, Jocko R., 30/VI/1963, A. R. Gaufin, 1 ♂, 3 ♀ (UU); Stillwater Co., Columbus, Yellowstone R., 25/VI/1966, J. R. Grierson, 2 ♂ (UU); Sweetgrass Co., Big Timber, Yellowstone R., 30/IV/1966, J. R. Grierson, 35 ♂, 37 ♀ (RWB). NEVADA: Clark Co., 5 mi. N. of Paradise Valley, Martin Crk., 18/VI/1967, D. M. Lehmkulh, 2 ♂, 4 ♀ (RWB); White Pine Co., Lehman Caves National Monument, 30/VI/1939, Thacker, 1 ♂, 1 ♀ (SJ). NEW MEXICO: Colfax Co., 6 mi. N.W. of Cimarron, Hwy. 64, 9/VI/1954, R. L. Wenzel, 1 ♂, 3 ♀ (SJ); Rio Arriba Co., San Juan R., 4/VII/1966, A. R. Gaufin, 1 ♂, 1 ♀ (RWB), 15 mi. N.W. of Tres Piedras, Hwy. 64, 7/V/1976, S. W. Szczytko and K. W. Stewart, 3 ♂, 7 ♀ (SWS & NTSU), S. of Chama, Hwy. 64, 7/V/1976, S. W. Szczytko and K. W. Stewart, 1 ♂, 3 ♀, 6 nymphs (SWS & NTSU); San Miguel Co., Las Vegas, Date ?, H. S. Barber, 1 ♀ (SJ), above Pecos, Hwy. 63, Pecos R., 4/VI/1977, S. W. Szczytko and K. W. Stewart, 2 ♂, 1♀, 3 nymphs (SWS & NTSU); Santa Fe Co., Santa Fe, 22/VI/1949, D. G. Denning, 1 ♂, 1 ♀ (SJ); Taos Co., 8 mi. W. of Ute Park, Hwy. 64, 7/V/1976, S. W. Szczytko and K. W. Stewart, 3 ♂, 2 ♀, 8 nymphs (SWS & NTSU). OREGON: Clatsop Co., 2 mi. E. Elsie, Nehalem R.,

11/VII/1964, S. G. Jewett, 5 ♂, 3 ♀ (SJ), 4 mi. N.E. Elsie, Red Bluff, Nehalem R., 12/V/1965, S. G. Jewett, 2 ♂, 2 ♀ (CU); Deschutes Co., Tumalo Reservoir, 24/VI/1954, H. H. Ross, 1 ♀ (INHS); Klamath Co., 12 mi. E. of Chiloquin, Sprague R., 1-3/VII/1951, B. Malkin, 4 ♂, 3 ♀ (UU); Lane Co., Willamette R., 25/VI/1946, S. G. Jewett, 8 ♀ (LCMNH), 15 mi. N. Lakeview, Crooked R., 7/VI/1955, R. Schuh, 1 ♂ (OSU[2]). SOUTH DAKOTA: Custer Co., Custer State Park., Iron Crk., 6/VII/1968, Harris and Cooley, 2 ♀, 1 nymph (RWB); Lawerence Co., Black Hills National Park, near Savoy, Rt. 14, 6/VII/1968, Harris and Cooley, 3 ♂, 4 ♀, 1 nymph (RWB), Spearfish, 27/VII/1940, T. H. and T. H. Frison, Jr., 2 ♀, 1 nymph (INHS). UTAH: Cache Co., Paradise, 14/VI/1938, Hardy and Stains, 1 ♂, 11 ♀ (INHS); Duchesne Co., Duchesne, Duchesne R., 3/VIII/1973, B. P. Stark and R. W. Baumann, 1 ♀ (BS); Emery Co., Stewart Station, 10/V/1975, Collector ?, 1 ♀ (RWB); Garfield Co., 3 mi. E. of Panguitch Lake, 12/VII/1961, G. F. Knowlton, 4 ♂, 10 ♀ (UU); Millard Co., Kanosh Canyon, 12/VIII/1946, G. F. Knowlton, 2 ♂, 3 ♀ (RWB), Kanosh Canyon, 27/V/1939, G. F. Knowlton and Harmston, 1 ♂, 1 ♀ (INHS), Maple Hollow Forest Camp, 11/VI/1959, Collector ?, 1 ♀ (UU), Kanosh Canyon, 1/VI/1977, S. W. Szczytko and K. W. Stewart, 20 ♂, 30 ♀, 21 nymphs (reared 8 ♂, 11 ♀), (SWS & NTSU); Rich Co., above Randolph, Big Crk., 21/VIII/1975, Reichert, 2 ♂, 7 ♀ (RWB); Salt Lake Co., Big Cottonwood Crk., 29/V/1953, G. F. Edmunds, 20 nymphs (RWB); Butterfield Canyon Crk., 1/VI/1977, S. W. Szczytko and K. W. Stewart, 48 nymphs (reared 21 ♂, 12 ♀), (SWS & NTSU); San Juan Co., Manti La Sal National Forest, Pack Crk., 12/V/1976, S. W. Szczytko and K. W. Stewart, 38 nymphs (reared 10 ♂, 8 ♀), (SWS & NTSU); Sevier Co., W. of Sevier, Hwy. 4, Clear Crk., 1/VI/1977, S. W. Szczytko and K. W. Stewart, 18 ♂, 23 ♀, 30 nymphs (SWS & NTSU); Summit Co., 1 mi. W. of Peoa, Weber R., 28/VII/1973, B. P. Stark, 3 ♂, 7 ♀ (UU), Henefer, 24/VI/1943, G. F. Knowlton, 1 ♂, 2 ♀ and exuvia (INHS), Silver Crk., 29/VI/1943, G. F. Knowlton and Telford, 4 ♂, 3 ♀ (INHS); Unitah Co., 8 mi. N. of Vernal, 22/VI/1949, I. L. Bell, 1 ♀ (RWB); Wasatch Co., near Heber, Center Crk., 7/VIII/1975, Sakamoto, 1 ♂, 3 ♀ (RWB), Trout Crk., 3/IV/1965, D. C. Hales, 2 nymphs (UU); Weber Co., Ogden Canyon, 18/VI/1938, M. C. Tanner, 1 ♀ (UU), Weber R., 24/III/1957, G. Smith, 3 nymphs (UU). WYOMING: Lincoln Co., Elbow Forest Camp, Hwy. 89, Snake R., 19/VII/1962, Collector ?, 1 ♀ (UU), La Barge, Green R., 17/VII/1962, Collector ?, 2 ♂ (UU), La Barge, Hwy. 189, La Barge Crk., 18/VII/1962, Collector ?, 7 ♂, 12 ♀ (UU), Silver Springs, Hwy. 189, Salt R., 19/VII/1962, Collector ?, 14 ♂, 22 ♀ (UU); Park Co., Yellowstone National Park, Firehole R., 6/VI/1946, Collector ?, 2 ♀ (UU); Sublette Co., N.W. of Daniel, Hwy. 187, Green R., 19/VII/1962, Collector ?, 2 ♀ (UU), Big Piney, Hwy. 189, Cottonwood Crk., 18/VII/1962, Collector ?, 4 ♂, 2 ♀ (UU), Pinedale, Pine Crk., 20/VII/1972, B. P. Stark, 1 ♂ (BS), Daniel, Hwy. 189, Horse Crk., 18/VII/1962, Collector ?, 2 ♀ (UU), N. of Cora, Willow Crk., 18/VII/1962, Collector ?, 1 ♀ (UU), N. of Daniel, Hwy. 189, Green R., 18/VII/1962, Collector ?, 6 ♂, 10 ♀ (UU); Teton Co., 1 mi. S. of entrance to Yellowstone National Park, Polecat Crk., 27/VI/1964, J. W. Richardson and S. L. Jensen, 1 nymph (UU); Unita Co., Evanston, Bear R., 16/VII/1962, Collector ?, 5 ♂ (UU), Fort Bridger, Groshen Crk., 21/VII/1967, R. W. Baumann, 1 ♀ (RWB).

Distribution. — CANADA: British Columbia. USA: California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, South Dakota, Utah and Wyoming (Fig. 2).

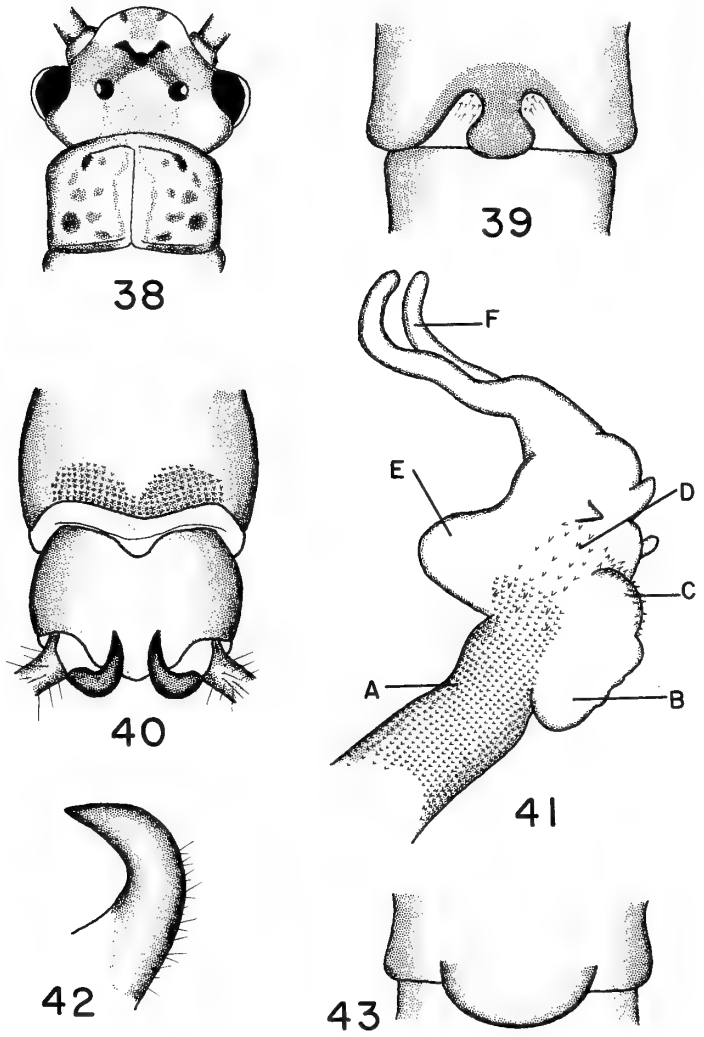
Diagnosis and Discussion. — *I. quinquepunctata* is most similar to *I. longiseta.* Males can be distinguished by the broader paraprocts, absence of 2 short finger-like membranous lobes on dorsum of aedeagus, presence of 2 large mesal lobes on aedeagus, and presence of hair-like setae on the 10th tergum. Females can be separated by the narrower deeply notched subgenital plate. Nymphs can be separated by the darker pigment pattern of the head, lack of rugosities on the pronotum, and by the continual dorsal fringe of long hairs after the 17th cercal segment, and absence of long posterior ventral hair. Ova can be distinguished by the triangular-shaped cross section of the anterior 1/2, and the non-elevated micropyles.

I. patricia Frison is placed in synonomy with *I. quinquepunctata* (Banks), based on our extensive holomorphological analysis and behavioral study. Part of the confusion surrounding *I. quinquepunctata* results from the lack of good character illustrations accompanying the original description, and paucity of verified specimens. Prior to our study, the type female was the only confirmed specimen available for comparison.

Two successive collecting trips were made in May, 1976 and Jun., 1977 to the type locality, Gallinas R. near Las Vegas, New Mexico, but no specimens were found. Installation of a dam, intensive irrigation uses, and probable pesticide pollution have drastically altered the ecology of the river since original collections, thereby eradicating or severely reducing populations. Ova from the type *I. quinquepunctata* female, and other females from the type locality and nearby streams, were compared with those from *I. patricia* paratypes from the South Dakota type locality and Utah streams. No discernible differences were found in the structure, chorionic sculpturing or micropyle arrangement in these eggs. Also, a comparison of adult genitalia of these specimens revealed no diagnostic character differences.

Study of many *I. quinquepunctata* aedeagii from diverse localities over its geographic range, revealed no variation in shape, lobation or spinulation. Those from the Pecos River, New Mexico (near the type locality) were identical to those from the Black Hills National Monument, South Dakota, near the type locality of *I. patricia.* No difference was noted in the species specific drumming signals of specimens studied from Colorado, New Mexico and Utah (unpublished concurrent study).

This species exhibits a large amount of morphological variation in male wing length, area of bipartite patches of long hair-like setae on the



FIGURES 38-43. — *I. katmaiensis.* 38. adult head and pronotum (scale: 1 mm = .05 mm). 39. male vesicle and 8th sternum (1 mm = .02 mm). 40. male terminalia, dorsal aspect (1 mm = .02 mm). 41. male aedeagus, lateral aspect, A. proximal stalk bearing concentrated small, stout spinulae, B. large flattened meso-posterior lobe, C. narrow band of long stout spinulae, D. scattered patch of very large stout spinulae, E. large anterior conical lobe, F. long tubular dorsal membranous processes (1 mm = .02 mm). 42. male paraproct, lateral aspect (1 mm = .01 mm). 43. female subgenital plate (1 mm = .05 mm).

9th and 10th terga, shape of vesicle on 9th sternum, shape of female subgenital plate, and general body size. At several localities many variations in these characters could be observed in one population. Males collected and reared from Piceance Crk., Rio Blanco Co., Colorado, were both macropterous and brachypterous, exhibited both vesicle shapes, and displayed variations in the area of setae on the 9th and 10th terga. The subgenital plate of females also exhibited a great amount of variation. No correlation between wing length and any of the variable characters was observed. The most stable diagnostic characters in all populations studies were the male paraprocts, aedeagus, ova, and the dumming signal.

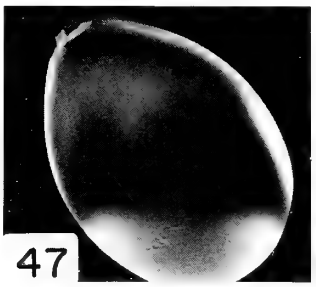
Dodds and Hisaw (1925) reported that *I. quinquepunctata* was distributed between 6,000-9,000′ in the Colorado Rockies, and Knight and Gaufin (1966) stated that *I. patricia* was a eurythermic stonefly species found between 6,800-9,400′. Ricker (1964) reported this species was typically distributed in the "eastern foothills and inter-mountain valleys and plateaus, rather than the main ranges" in Canada, and was found in large warm river systems. No studies on the life history or general biology have been done for this species. Based on the material examined emergence begins in early May in southern latitudes and continues until early Aug., with the largest numbers taken from the last of Jun. to the first of Jul.

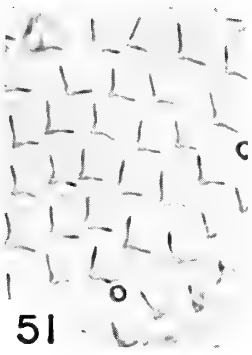
INDIVIDUAL SPECIES (not assigned to group)

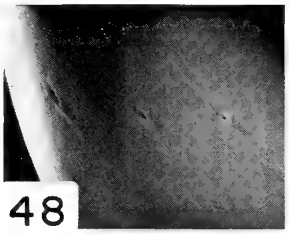
Isoperla katmaiensis NEW SPECIES

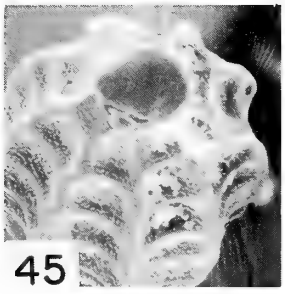
Male. — Brachypterous. Length of forewings 5.3 mm; length of body 9.8-11.4 mm. General body color dark brown. Lateral ocelli of head connected to anterior ocellus by narrow black band, interocellar area medium brown, wide medium brown band extending from back of head to anterior ocellus and laterally to base of antennae, anterior frons with medium brown patch (Fig. 38). Pronotum medium brown, variable-width light median stripe, rugosities rounded, dark brown to black (Fig. 38). Wings fumose, veins dark brown. Abdominal terga with 8 rows of longitudinal dots, 2 mesal and 3 each laterally, median rows most prominent. Ninth tergum with bipartite patch of stout spinulae on posterior margin (Fig. 40). Tenth tergum with narrow, light unsclerotized median trough (Fig. 40). Posterior margin of cercal segments with whorl of medium-length hairs and one long dorsal and ventral hair. Vesicle distinctively petiolate, evenly rounded posteriorly, darker than rest of segment, base with narrow dark band extending to lateral margins of segment (Fig. 39). Paraprocts long and stout, tapering to points apically and deflecting outward, curving anteriorly over 1/4 10th tergum, posterior margin with long fine hairs (Figs. 40 & 42). Aedeagus entirely membranous, petiolate, 2 long, tubular,

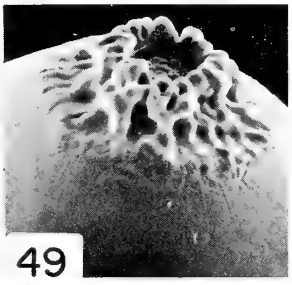
FIGURES 44-53. — Scanning electron micrographs of *Isoperla, Cascadoperla* ova, and light micrographs of aedeagal armature. Figs. 44-46 & 50. *Cascadoperla tric-*

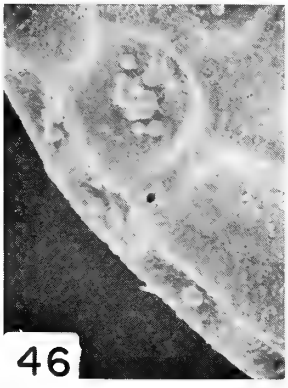


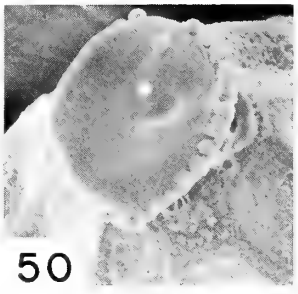


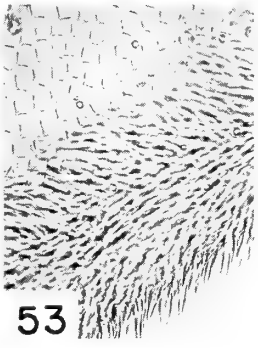












tura. 44. whole ova 200×. 45. dorsal view of collar and longitudinal ridges 400×. 46. detail of micropyle 1000×. 50. detail of collar 1000×: Figs. 47-49. *I. katmaiensis*. 47. whole ova 200×. 48. detail of micropyles 700×. 49. detail of collar 700×: Figs. 51-53. *I. tilasqua*. 51. light micrograph — small stout spinulae on aedeagus 800×. 52. light micrograph — small fine hair-like spinulae on aedeagus 800×. 53. light micrograph — long hair-like spinulae on aedeagus 800×.

Magnifications represent original values before reduction of plate.

membranous processes at apex (Fig. 41F), dorsal section void of spinulae, large conical lobe on anterior margin void of spinulae (Fig. 41E), large flattened lobe on posterior margin with narrow dorsal patch of long stout spinulae (Fig. 41B & C), one single and one double small posterior finger-like lobes above large flattened lobe, proximal stalk bearing heavy concentration of small stout spinulae (Fig. 41A), scattered patch of very large stout spinulae on mesal section (Fig. 41D), small triangular lobe above stout spinulae patch.

Female. — Macropterous. Length of forewings 13.1-16.1 mm; length of body 11.4-14.3 mm. General body color and head-pronotal pigment patterns similar to male. Subgenital plate wide at base, semicircular, produced approximately 1/4 length of 9th sternum (Fig. 43).

Nymph. — UNKNOWN.

Ova. — General shape oval, cross section circular (Fig. 47). Color dark brown. Length .28 mm; width .20 mm. Collar well developed, ornate, with thickened, elevated irregular ridges forming apical depression (Fig. 49). Chorion entirely smooth. Micropyles arranged in 2 sets of 3 in a row near bottom 1/3 on one side, elevated sperm guides below each micropyle (Figs. 47 & 48).

Material examined. — TYPES: Holotype ♂, and allotype ♀, USA, ALASKA, Katmai National Monument, Brooks R., at BCF Camp, 4/VII/1969, K. J. Raedeke (RWB), (types deposited at USNM). Paratypes *USA:* ALASKA, Katmai National Monument, Brooks R., at BCF Camp, K. J. Raedeke (RWB), 18/VI/1969, 5 ♂, 2 ♀, 20/VI/1969, 5 ♂, 1 ♀, 24/VI/1969, 5 ♂, 1 ♀, 4/VII/1969, 10 ♂, 2 ♀, 17/VII/1969, 3 ♂ (paratypes deposited at USNM, RWB, NTSU & SWS).

Distribution. — USA: Alaska (Fig. 54).

Diagnosis and Discussion. — This species is most similar to *I. jewetti.* Males can be differentiated by the darker general body color and head-pronotal pigment patterns, absence of two dark brown patches on the 10th tergum, petiolate shape of vesicle, presence of a narrow, light unsclerotized median trough on the 10th tergum, shorter stout paraprocts, presence of 2 long, tubular processes on apex of the aedeagus, and patterns, shapes, and sizes of aedeagul spinulae. Females can be differentiated by the general darker body color and head-pronotal pigment patterns and subgenital plate (in some specimens the subgenital plate is very similar). Ova can be separated by the ornate collar with thickened, elevated, irregular ridges, entirely smooth chorion and lack of chorionic punctations.

It is not placed in any species group at this time due to the uniqueness of the ova. The ova are unlike any known *Isoperla* and are similar to some perlid ova. It is closest to the *I. quinquepunctata* complex in that males have an entirely membranous aedeagus and bipartite patch of spinulae on the 9th tergum, and the female subgenital plate is broadly rounded.

This species is apparently rare and restricted to the extreme northern part of the North American Continent (Fig. 54), and probably represents one of the limits of the northwest range of the genus *Isoperla* in North America.

No data on the life history or general biology are available. Based on the material examined, emergence occurs from mid-Jun. to mid-Jul.

Etymology. — This species is named after the type locality from the Katmai National Monument in Alaska.

SPECIES GROUP B

Isoperla phalerata complex

This group is composed of *I. phalerata* (Needham) and *I. pinta* Frison. Both species share the following characteristics: 1. male aedeagus entirely

FIGURE 54. — Distribution of *I. katmaiensis*.

membranous, bearing a large patch of small stout spinulae, and many lobes; 2. male 9th tergum with either a single or bipartite patch of stout spinulae; 3. reduced male vesicle; 4. sharply tapered paraprocts with acute ventral spine; 5. broad female subgenital plate, rounded posteriorly with a median notch; 6. contrasting dark brown and yellow head-pronotal pigment patterns in nymph and adult; 7. nymphal pronotum with angles rounded and fringed with small stout setae; 8. nymphal femorae, tibiae, and tarsi with a dorsal fringe of long fine hairs; 9. abdominal terga with 3 longitudinal stripes and 8 longitudinal rows of dots; 10. ova with well-developed collar and chorionic ridges; 12. sculpturing of chorion variable; and 3. micropyles elevated and arranged in pairs or threes near bottom 1/3, on one side.

The group is distributed from South Dakota to California, and New Mexico to Canada (Fig. 55). Both species inhabit creeks and small- to medium-sized rivers. Emergence continues from May until the end of Jul., and both species are thought to undergo univoltine life cycles.

Isoperla phalerata (Needham)

Dictyogenus? phaleratus Needham, 1917, 43:485. Holotype ♀; New Mexico, USA (CU #1,151), (wings and female genitalia).
Perla phalerata, Needham and Claassen, 1925, 2:91 (female genitalia and ova).
Perla phalerata, Claassen, 1940, 232:144.
Perliphanes phaleratus, Banks, 1947; 54:278.
Isogenus phaleratus, Ricker, 1952, 18:131 (female head, wings and genitalia).
Isoperla phalerata, Jewett, 1954, 11:548. Allotype ♂, Grand Ronde R., La Grane, Union Co., Oregon (CAS) (male genitalia).
Isoperla phalerata, Illies, 1966:415.
Isoperla phalerata, Zwick, 1973:250.
Additional references: *Isoperla phalerata,* Jewett, 1959 (male genitalia), Gaufin, 1964b; Logan and Smith, 1966; Stewart et al., 1974; Baumann et al., 1977 (wings).

Male. — Macropterous-brachypterous. Length of forewings (macropterous) 9-11 mm; length of body 8-11 mm; length of forewings (brachypterous) 5-6 mm; length of body 10-11 mm. General body color medium brown. Head-pronotal pigment pattern with contrasting dark brown and bright yellow areas. Lateral ocelli connected to anterior ocellus by "n"-shaped band of dark brown pigmentation; thin dark "u"-shaped band connecting anterior ocellus with thin dark bands extending from base of antennae; short black bands extending backward from each antennal base; interocellar space light yellow; frons with variable dark band (Fig. 56). Pronotum with median yellow stripe and longitudinal dark brown patches (Fig. 56). Cross veins usually present in radial sector of forewings (variable, in one or both wings, or none) (Fig. 60). Ninth tergum with bipartite patches of small stout spinulae at posterior margin; median anterior 1/2 with dark brown patch (Fig. 59). Tenth tergum light yellow with median dark spot (Fig. 59). Abdominal terga with 8 rows of longitudinal dots, 2 mesal, and 3 each laterally. Paraprocts tapering to

blunt tips, with acute apical ventral spine (Fig. 58); appearing sharp from dorsal view (Fig. 59); recurving anteriorly over 1/4 10th tergum, and deflecting slightly outward; surface bearing small fine hairs (Figs. 58 & 59). Vesicle reduced, not projecting beyond anterior margin of 9th sternum; wider at base than apex; broadly rounded posteriorly; darker than rest of segment (Fig. 57). Aedeagus entirely membranous; one median posterolateral lobe with small, fine scattered spinulae (Fig. 62A); one small posterodorsal, 2 dorsal and 1 anterodorsal lobes devoid of spinulae (Fig. 62); mesal section covered with dense, small, stout spinulae (Fig. 62B); patch of longer, slender spinulae above stout spinulae at posterodorsal margin, below small anterodorsal lobe (Fig. 62C).

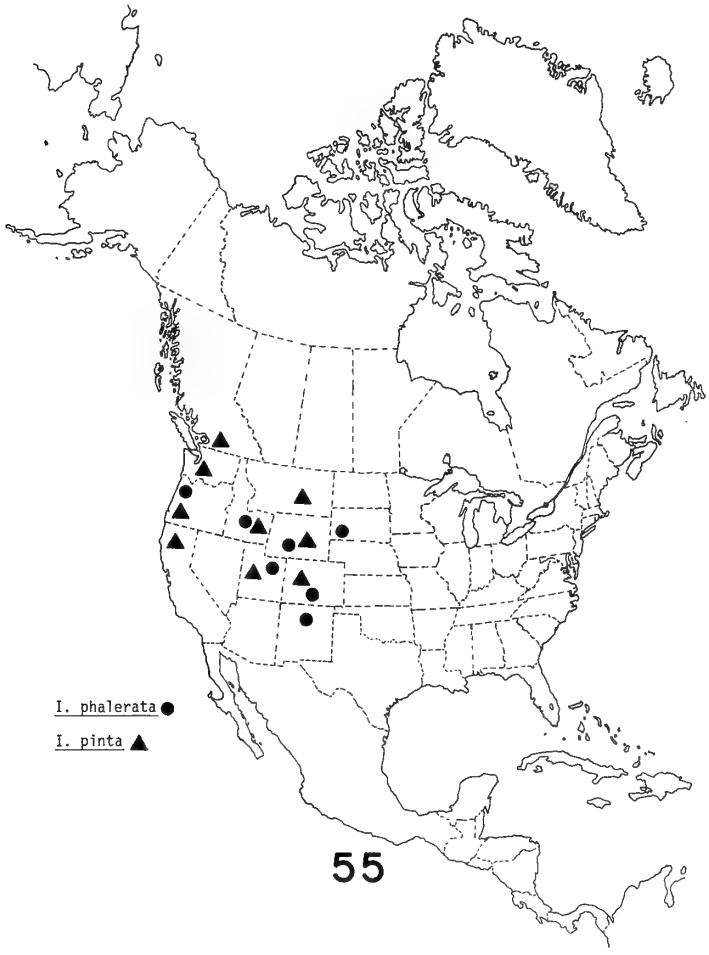


FIGURE 55. — Distribution of the *I. phalerata* complex.

Female. — Macropterous. Length of forewings 11-15 mm; length of body 9-12 mm. General body color, and head-pronotal pigmentation patterns similar to male. Subgenital plate broad at base, produced 3/8 length of 9th sternum, rounded posteriorly with a slight median emargination (variable, from deeply notched to absent) (Fig. 61).

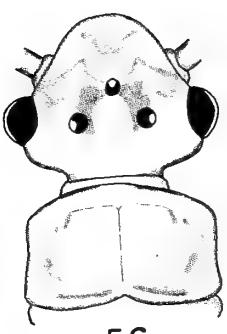
Nymph (Reared). — Length of mature male nymph 11-14 mm; length of mature female nymph 13-16 mm. Dorsum of head with dark brown transverse pigment band extending between antennal bases; band extended backward to lateral ocelli. Interocellar space light. Occipital ridge, with medium, stout spinulae (Fig. 63). Pronotum fringed with small stout setae, 1 or 2 long hairs irregularly placed; angles broadly rounded (Fig. 63). Abdominal terga with 3 longitudinal stripes, 2 lateral and 1 mesal, and 8 rows of longitudinal dots, 2 mesal and 3 each laterally. Femora with dorsal fringe of long fine hairs; tibiae with dense fringe, and tarsi with less concentrated fringe. Posterior margin of cercal segments with whorl of small stout hairs; incomplete dorsal fringe of medium length hairs on segment 16; continual dorsal fringe on 17th and remaining segments; 1 long ventral hair at posterior margin after 20th segment.

Ova. — General shape oval, cross section circular (Fig. 68). Color light brown. Length .28 mm; width .20 mm. Collar well developed (Figs. 68, 69 & 71). Chorion bearing numerous, evenly spaced punctations, chorionic ridges elevated slightly (Figs. 68 & 69). Micropyles raised with large openings, grouped 3 in a row near bottom 1/3, on one side (Fig. 70).

Material examined. — TYPES: Holotype ♀, NEW MEXICO: Date ?, Collector ? (CU #1,151). Allotype ♂, OREGON: Union Co., La Grande, Grande Ronde R., 6/VI/1948, D. G. Denning (CAS). Additional specimens — *USA:* COLORADO: Huerfano Co., Hwy. 160, 2 mi. E. of La Veta Pass, 6/V/1976, S. W. Szczytko and K. W. Stewart, 2 ♀, 3 nymphs, 1 exuvia (SWS & NTSU); Jackson Co., S.W. of Walden, Hwy. 14, Grizzly Crk., 9/V/1976, S. W. Szczytko and K. W. Stewart, 10 nymphs (reared 3 ♂), (SWS & NTSU); County ?, Willow Crk. Pass, 2/VII/1962, R. and K. Dreisback, 1 ♀ (WR). IDAHO: Adams Co., 15 mi. N. of New Meadows, Hwy. 95, Little Salmon R., 17/VI/1964, Collector ?, 2 ♂ (RWB). NEW MEXICO: Colfax Co., Ute Park, Cimarron Canyon, 12/VI/1956, Collector ?, 1 ♂, 3 ♀ (WR); Rio Arriba Co., 15 mi. N.W. of Tres Piedras, Hwy. 64, 6/V/1976, S. W. Szczytko and K. W. Stewart, 2 ♂, 3 ♀, 3 exuviae (SWS & NTSU). OREGON: Harney Co., Trout Crk., 23/V/1950, Fender and S. G. Jewett, 1 ♂, 2 ♀ (SJ), Frenchglen, 26/VI/1951, B. Malkin, 2 ♀ (SJ); Lake Co., Chandler State Park, 27/V/1957, B. Malkin, 2 ♂ (SJ), Chewaucan R., 18/VI/1955, J. Schuh, 2 ♂, 4 ♀ (SJ). UTAH: Garfield Co., Panguitch Crk., 27/VI/1967, G. F. Knowlton, 2 ♀ (WR).

Distribution. — USA: Colorado, Idaho, New Mexico, Oregon, South Dakota, Utah, and Wyoming (Fig. 55).

FIGURES. 56-63. — *I. phalerata.* 56. adult head and pronotum (scale: 1 mm = .06 mm). 57. male vesicle and 8th sternum (1 mm = .06 mm). 58. male paraproct, lateral view (1 mm = .02 mm). 59. male terminalia, dorsal aspect (1 mm = .07 mm). 60. female left forewing, A. radial sector, B. cross veins of radial sector (1 mm = .31 mm). 61. female subgenital plate (1 mm = .08 mm). 62. male



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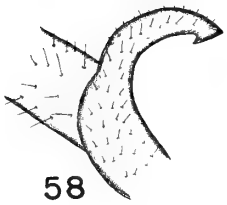

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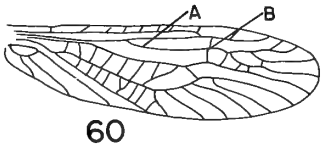

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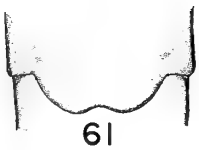

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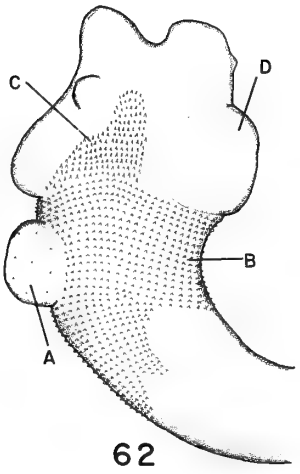

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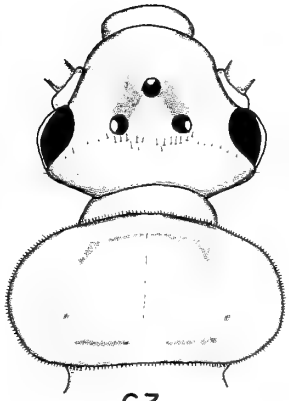


63

aedeagus, lateral aspect, A. mesoposterior lobe bearing small, fine scattered spinulae, B. dense small stout spinulae, C. long slender spinulae, D. anterodorsal lobe (1 mm = .05 mm). 63. nymph head and pronotum (1 mm = .05 mm).

Diagnosis and Discussion. — This species is very similar to *I. pinta.* Males can be distinguished by the lighter pigment patterns of the head and pronotum, variable presence of crossveins in the radial sector of the forewings, narrower vesicle, less curved paraprocts, shape of spinulae pattern on 9th tergum, and spinulae pattern of the aedeagus. Females can be differentiated by the lighter pigment patterns of the head and pronotum, variable presence of crossveins in radial sector of the forewings, and longer, narrower subgenital plate. Nymphs can be separated by the lighter pigment patterns of the head and pronotum, presence of occipital ridge of spinulae, broadly rounded angles of the pronotum, and absence of a long dorsal hair at posterior margin of each cercal segment. Ova can be distinguished by the small, uniform chorionic punctations, lower chorionic ridges, and absence of highly elevated, ornate multiple opening micropyles. The distribution of *I. phalerata* follows *I. pinta* closely except that it is not found as far North, and both species inhabit creeks and medium-size river systems (Fig. 55).

Authorship and type locality of this species have been confusing and incorrectly cited since its inception. The original description appeared in a paper by Smith (1917). She hesitantly placed it in *Dictogenus* and gave J. G. Needham authorship for the species, indicating that the description was quoted from his manuscript. Two specimens were mentioned in the text, one female from New Mexico which was designated as the holotype, and another female from Colorado (?/VI/1907, T. D. A. Cockerell). Needham and Claassen (1925) later reported that the specimen from Colorado was *Perla modesta.*

No life history or biological studies have been done. Based on the material examined, emergence begins in early May and continues until late Jul., with the largest numbers taken in mid-Jul.

Isoperla pinta Frison

Isoperla pinta Frison, 1937, 21:92. Holotype ♂; Floras Crk., Curry Co., Oregon, USA (INHS), allotype, Corvallis, Benton Co., Oregon, USA (INHS); (male head-pronotal pigment pattern, forewing, and genitalia; female subgenital plate; nymphal maxilla, labium, and habitus).

Isoperla tokula Hoppe, 1938, 4:157. Holotype ♂, and allotype ♀, Tokul Crk., Washington, USA (TBM); (male and female genitalia). Syn. Frison, 1942.

Isoperla pinta, Claassen, 1940, 232:204.

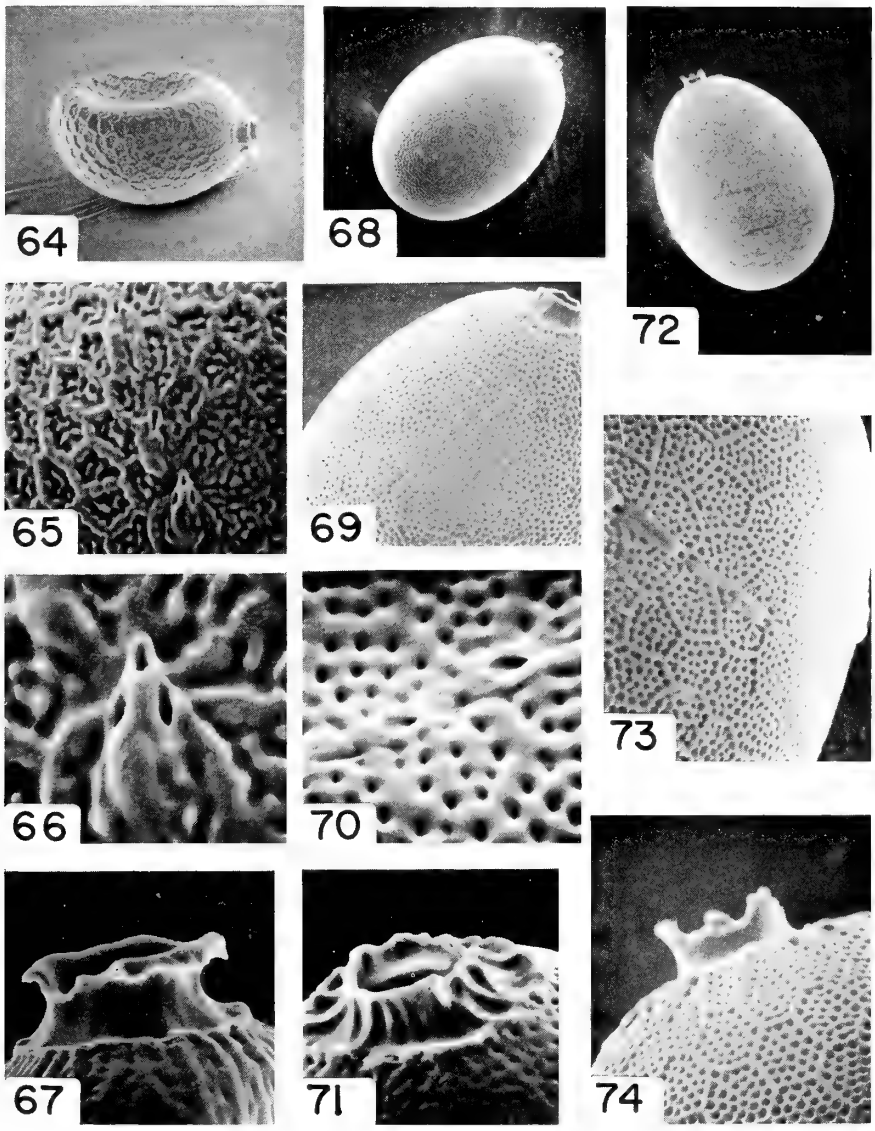
Isoperla pinta, Frison, 1942, 22:337. Syn. indicated.

Occiperla pinta, Banks, 1947, 54:280 (femur).

Isoperla pinta, Illies, 1966:416.

Isoperla pinta, Zwick, 1973:250.

Additional references: *Isoperla pinta,* Ricker, 1939 and 1943; Gaufin, 1955; Jewett, 1959, 1960 (male and female genitalia); Gaufin, 1964; Ricker, 1964; Knight



FIGURES 64-74. — Figs. 64-67. *I. pinta.* 64. whole ova 200×. 65. detail of chorion 700×. 66. detail of ornate micropyle 2000×. 67. detail of collar 1000×: Figs. 68-71. *I. phalerata.* 68. whole ova 200×. 69. detail of chorion 400×. 70. detail of micropyles 1000×. 71. detail of collar 1000×: Figs. 72-74. *I. petersoni.* 72. whole ova 200×. 73. detail of chorion and micropyle ridge 1000×. 74. detail of collar 1000×.

Magnifications represent original values before reduction of plates.

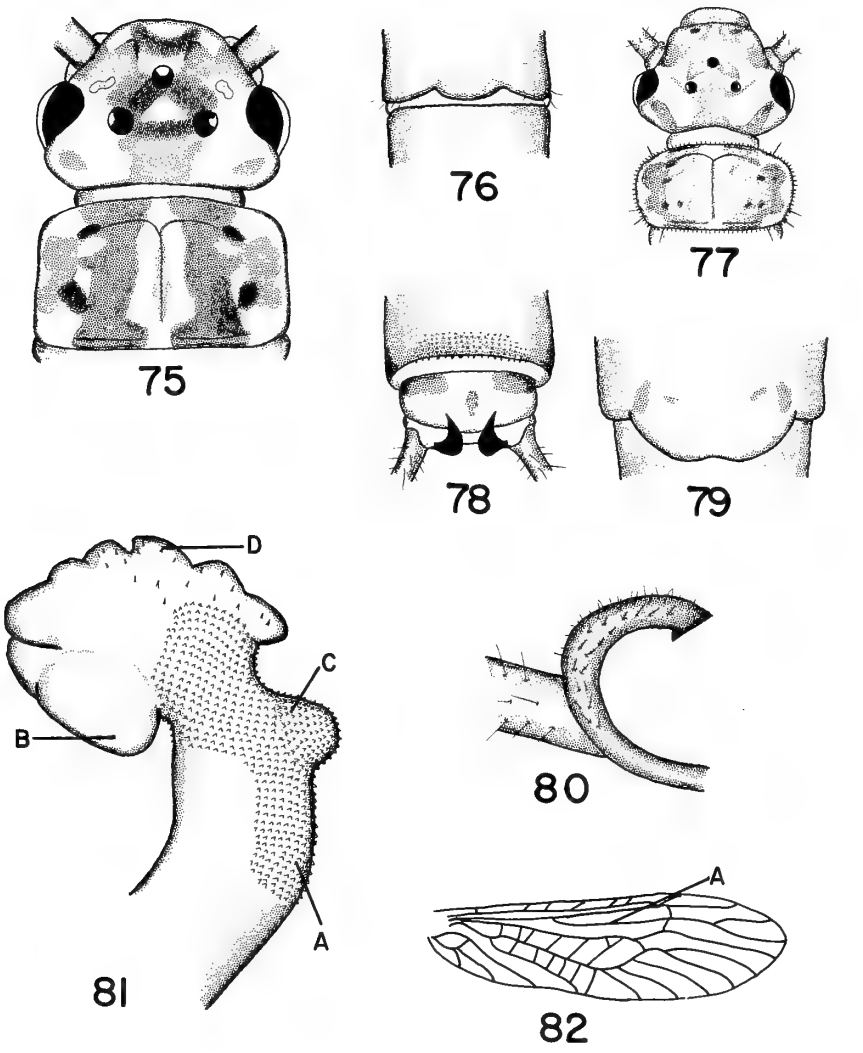
et al., 1965b (ova); Gaufin et al., 1966 (male and female genitalia); Logan and Smith, 1966, Knight and Gaufin, 1966, 1967; Newell, 1970; Baumann, 1971; Gaufin et al., 1972 (male and female genitalia); Ricker and Scudder, 1975; Baumann et al., 1977 (male and female genitalia).

Male. — Macropterous. Length of forewings 10-12 mm; length of body 9-11 mm. General body color medium brown. Head-pronotal pigment pattern with contrasting black, or dark brown and light yellow areas. Ocelli with dark brown pigment forming equalateral triangle; surrounded interocellar space light yellow; wide medium brown band extending from base of antennae to anterior ocellus; anterior frons with dark brown band (Fig. 75). Pronotum with median yellow stripe, 2 wide, longitudinal black bands, and 2 mesolateral brown patches (Fig. 75). Crossveins absent from radial sector of forewings (Fig. 82). Ninth tergum with band of stout spinulae on posterior margin. Posterior 1/2, and median of 10th tergum light yellow, with dark brown mesal spot (Fig. 78). Abdominal terga with 8 rows of longitudinal dots, 2 mesal, and 3 each laterally. Paraprocts wide at base tapering apically to blunt tips with acute ventral spines that appear sharp from dorsal view; recurving anteriorly over 1/3 10th tergum, deflecting outward strongly; dorsal surface bearing small fine hairs (Figs. 78 & 80). Vesicle reduced, not projecting beyond anterior margin of 9th sternum; wider at base than apex, broadly rounded posteriorly and darker than rest of segment (Fig. 76). Aedeagus entirely membranous, several small lobes at apex, one mesal posterolateral lobe void of spinulae (Fig. 81B), one mesoposterior lobe covered with small stout spinulae (Fig. 81C), apex with scattered long hair-like spinulae (Fig. 81D), large patch of concentrated small, stout spinulae covering posterior margin and mesal section (Fig. 81A).

Female. — Macropterous. Length of forewings 12-14 mm; length of body 10-12 mm. General body color, and head-pronotal pigment patterns similar to male. Subgenital plate broad at base, produced 1/4 length of 9th sternum, rounded posteriorly with a shallow emargination (Fig. 79).

Nymph. — Length of mature male nymph 11-13 mm; length of mature female nymph 14-16 mm. Dorsum of head with median dark brown band extending from occiput to lateral ocelli, with narrow "Y"-arms extending anterolaterally behind lateral ocelli; anterior and lateral ocelli connected by 2 dark brown triangles, interocellar space light yellow, dark brown pigment pattern continuing to base of antennae and anterior margin of head, encircling 2 light yellow lateral spots on anterior frons; 2 heavy dark brown bands extending from occiput to back of compound eyes (Fig. 77). Pronotum with median yellow stripe, contrasting patches of dark brown and yellow pigmentation; margin fringed with short setae, occasional long setae near corners; angles moderately rounded (Fig. 77). Abdominal terga with 3 longitudinal stripes, 2 lateral and one mesal, and 8 rows of longitudinal stripes, 2 mesal, and 3 each laterally. Femora, tibiae, and tarsi with dorsal fringe of long fine hairs; dark brown band on femora before apex and on tibiae near proximad. Posterior margin of cercal segments with whorl of small, stout hairs; one long dorsal hair at posterior margin from 1st segment, one long ventral hair at posterior margin, and complete dorsal fringe of long hairs after 18th segment.

Ova. — General shape oval, cross section circular (Fig. 64). Color light brown. Length .27 mm; width .19 mm. Collar well developed and expanded apically (Figs. 64 & 67). Chorion ornate with elevated, thickened ridges forming distinct hexagonal shaped depressions with smaller, largely unconnected ridges inside (Figs. 64,



FIGURES 75-82. — *I. pinta.* 75. adult head and pronotum (scale: 1 mm = .05 mm). 76. male vesicle and 8th sternum (1 mm = .05 mm). 77. nymph head and pronotum (1 mm = .12 mm). 78. male terminalia, dorsal aspect (1 mm = .05 mm). 79. female subgenital plate (1 mm = .05 mm). 80. male paraproct, lateral aspect (1 mm = .01 mm). 81. male aedeagus, lateral aspect, A. large patch of small stout spinulae, B. large rounded anterior lobe, C. small mesoposterior lobe, D. scattered, long hair-like spinulae (1 mm = .03 mm). 82. female left forewing, A. radial sector (1 mm = .20 mm).

65 & 66). Micropyles ornate, elevated with one to several openings, grouped 3 in a row near bottom 1/3, on one side (Figs. 65 & 66).

Material examined. — TYPES: *I. pinta,* Holotype ♂, OREGON: Curry Co., Floras Crk., 20/V/1933, R. Dimick (INHS); allotype, OREGON: Benton Co., Corvallis, 5/V/1936, N. F. Larson (INHS). Paratypes; *CANADA* — BRITISH COLUMBIA: Cultus Lake, 24/IV/1935, W. E. Ricker, 1 ♀ (OSU[2]), Cultus Lake, 18/V/1933, W. E. Ricker, 1 ♂ (INHS), Cultus Lake, 13/V/1935, W. E. Ricker, 2 ♂, 3 ♀ (INHS), Cultus Lake, 24/IV/1935, W. E. Ricker, 2 ♂, 2 ♀ (INHS). *USA* — OREGON: Benton Co., Alsea, near Mill Crk., Alsea R., 22/V/1933, R. Dimick, 1 ♀ (INHS); Douglas Co., Winchester, N. Umpqua R., 22/III/1933, R. Dimick, 1 ♀ (INHS). Additional specimens — *CANADA* — BRITISH COLUMBIA: Cultus Lake, Sweltzer Crk., 2&4/VI/1937, W. E. Ricker, 71 ♂, 67 ♀ (WR), Cultus Lake, Sweltzer Crk., 8/IV/1937, W. E. Ricker, 27 nymphs (INHS), Cultus Lake, Sweltzer Crk., 13/III/1937, W. E. Ricker, 17 nymphs (WR), Cultus Lake, Sweltzer Crk., 26/IV/1937, W. E. Ricker, 2 ♂, 3 ♀ (WR), Cultus Lake, Reservoir Crk., 3&28/V/1935, W. E. Ricker, 1 ♂, 1 ♀ (INHS), Cultus Lake, Hatchery Crk., 16/V/1937, W. E. Ricker, 3 ♂, 6 ♀ (WR), Vedder Crossing, 8/V/1937, W. E. Ricker, 1 ♀ (WR). *USA* — CALIFORNIA: Carmel Co., Locality ?, 23/V/1919, E. P. Van Duzee, 1 ♀ (CU); Lake Co., Anderson Springs, 30/IV/1955, R. Leuschner, 1 ♀ (WR); Merced Co., Merced R., 9/V/1937, P. W. C., 1 ♂, 1 ♀ (INHS); Santa Cruz Co., near Felton, 7/VI/1976, D. G. Denning, 1 ♀ (RWB); Trinity Co., Indian Crk., at mouth of Trinity R., 2/III/1955, S. G. Jewett, 1 ♂, 1 ♀ (UU). COLORADO: Grand Co., Parshall, Hwy. 40, Troublesome Crk., 13/VI/1964, Collector ?, 1 ♂ (UU), N. of Granby, Hwy. 40, Colorado R., 27/VI/1962, Collector ?, 1 ♀ (UU); Routt Co., 10 mi. E. of Craig, Yampa R., 18&20/VI/1968, B. R. Oblad, 2 ♂, 4 ♀ (UU), 1 mi. above Peterson's Ranch, Yampa R., 27/VI/1968, B. R. Oblad, 1 ♀ (UU), Steamboat Springs, Yampa R., 26/VI/1962, Collector ?, 1 ♂, 1 ♀ (UU), Steamboat Springs, Yampa R., 17/III/1968, B. R. Oblad, 2 nymphs (UU). IDAHO: Fremont Co., 5 mi. S. of Island Park, Hwy. 191, Snake R., 23/VI/1964, J. W. Richardson and S. L. Jensen, 3 ♀ (UU); Valley Co., 10 mi. S. of Cascades, Hwy. 15, Big Crk., 17/IV/1963, Collector ?, 1 ♂, 1 ♀ (RWB). MONTANA: Lewis and Clark Co., Arrastra Crk., 1/VII/1969, R. L. Newell, 1 ♀ (UU); Missoula Co., Bunkhouse Bridge, Bitterroot R., 15/III/1969, B. R. Oblad, 1 nymph (UU); Teton Co., 2 mi. W. of Tetonia, Hwy. 33, Teton R., 22/VI/1964, J. W. Richardson and S. L. Jensen, 13 ♂, 20 ♀ (UU). OREGON: Benton Co., Philomath, Woods Crk., 24/IV/1936, W. M. Graf, 1 ♂ (INHS), Corvallis, 27/IV/1938, W. M. W., 2 ♂ (INHS); Klamath Co., 12 mi. E. of Chiloquin, Sprague R., 3/VII/1951, B. Malkin, 8 ♂, 9 ♀ (SJ), 12 mi. E. of Chiloquin, Sprague R., 1-3/VIII/1951, B. Malkin, 2 ♂, 1 ♀ (LCMNH), Clatsop Co., Youngs R., 1/V/1940, S. G. Jewett, 7 ♂, 24 ♀ (SJ), 4 mi. N.E. of Elsie, at Red Bluff, Nehalem R., 10/V/19ɔɔ, S. G. Jewett, 1 ♂ (CU); Douglas Co., Cow Crk., at mouth of Quines R., 5/IV/1968, S. G. Jewett, 1 ♀ (RWB); Lane Co., Indian Crk., 29/III/1940, S. G. Jewett, 2 ♂, 2 ♀ (UU). UTAH: Garfield Co., Asay Crk., 25/III/1959, A. R. Gaufin, 9 nymphs (UU); Peoa, Weber R., 19/II/1966, Collector ?, 1 nymph (UU); Ogden, Weber R., 25/V/1939, M. C. Tanner, 1 nymph (INHS). WYOMING: Carbon Co., Riverside, Madison R., 29/II/1964, Heaton, 6 nymphs (UU); Lincoln Co., Hwy. 189, La Barge Crk., 18/VII/1962, Collector ?, 1 ♀ (UU); Park Co., Yellowstone National Park, Norris Junct., 9/VI/1942, Collector ?, 1 ♂, 1 ♀ (RWB); Sublette Co., Daniel, Green R.,

19/VII/1972, B. P. Stark, 1 ♂ (BS), N.W. of Daniel, Hwy. 187, Green R., 19/VII/1962, Collector ?, 1 ♂, 1 ♀ (RWB), Big Piney, Hwy. 189, S. Piney Crk., 18/VII/1962, Collector ?, 2 ♀ (UU).

Distribution. — CANADA: British Columbia; USA: California, Colorado, Idaho, Montana, Oregon, Utah, Washington, and Wyoming (Fig. 55).

Diagnosis and Discussion. — *I. pinta* is closely allied with *I. phalerata* (see diagnosis and discussion under *I. phalerata*).

Knight and Gaufin (1966) reported that *I. pinta* was a stenothermic stonefly limited to altitudes below 8,500 feet. Knight and Gaufin (1967) found that *I. pinta* occurred in stony rivers, constant rivers, or sluggish rivers, and was associated most frequently with *Capnia limata* Frison, and *Utacapnia logana* (Nebeker and Gaufin) in the Gunnison River drainage system in Colorado.

No studies on the life history or general biology have been done. Based on the material examined, emergence begins in late Apr. along the Pacific Coast, and continues until mid-Jul. in the Central and Southern Rockies, with peak emergence occurring mid-Jun. This species inhabits creeks and medium-size rivers.

SPECIES GROUP C

Isoperla sobria complex

This group is composed of *I. sobria* (Hagen), *I. gravitans* (Needham and Claassen), and a new species *I. tilasqua*. *I. ebria* (Hagen) is not included here since our study of the female and ova indicate that it is a synonym of *I. sobria*. These species all share the following characteristics: 1. large body size and dark pigment patterns; 2. male aedeagus entirely membranous, tubular, usually bearing one large patch or band of small, stout spinulae, and one or more patches of longer hair-like spinulae; 3. male vesicle usually reduced or obsolescent; 4. female subgenital plate truncate or broadly rounded, wide at base; and 5. ova with well-developed collar and chorion bearing evenly spaced small punctations; chorionic ridge development variable from slight to highly elevated.

The group is distributed from New Mexico, Colorado, Utah and Northern California, northward into Canada (Fig. 83). Species inhabit creeks and small- to medium-sized rivers. Emergence occurs from early Apr. until early Aug., and all are thought to undergo univoltine life cycles.

Isoperla sobria (Hagen)

Perla sobria Hagen, 1874, 7:577. Holotype ♀; Colorado mountains, Colorado, USA (MCZ #247).

Perla ebria, Hagen, 1874, 7:577. Holotype ♀; Colorado mountains, Colorado, USA (MCZ #248). **NEW SYNONYMY.**
Perlinella sobria, Banks, 1902, 34:123.
Isoperla ebria, Banks, 1907a:13.
Clioperla ebria, Needham and Claassen, 1925, 2:141 (male and female genitalia).
Clioperla sobria, Needham and Claassen, 1925, 2:143 (female genitalia).
Clioperla ebria, Claassen, 1940, 232:196.
Clioperla sobria, Claassen, 1940, 232:196.
Isoperla ebria, Ricker, 1943, 12:121 (adult and nymph head and pronotum, nymphal maxilla and habitus, and female genitalia).
Isoperla ebria, Illies, 1966:401.

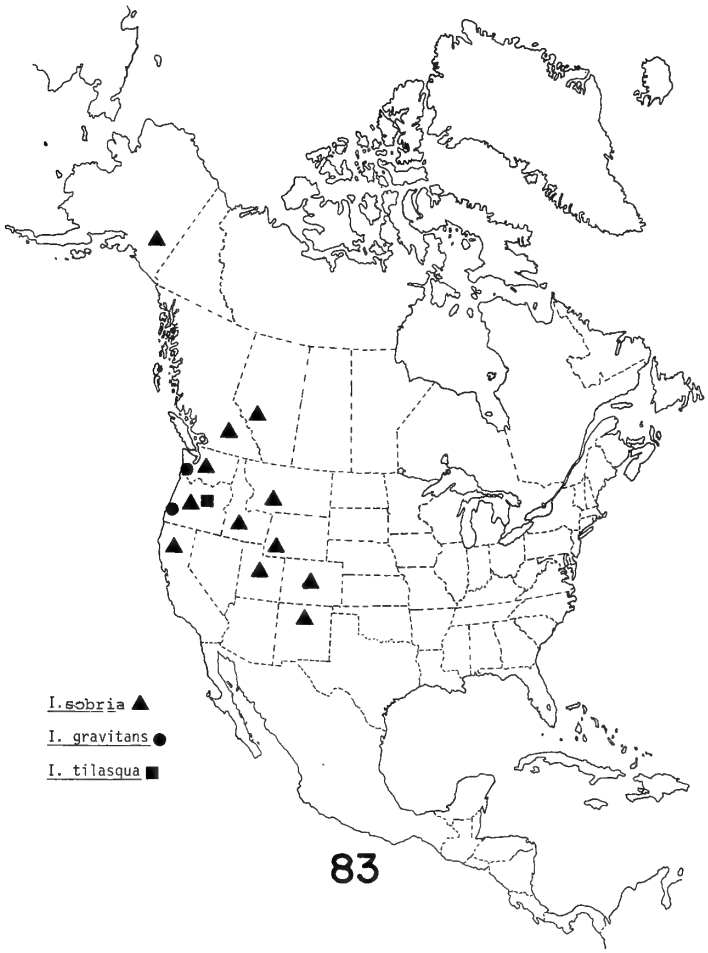


FIGURE 83. — Distribution of the *I. sobria* complex.

Isoperla sobria, Illies, 1966:240.
Isoperla ebria, Zwick, 1973:244.
Additional references: *Isoperla ebria,* Banks, 1907b; Dodds and Hisaw, 1929; Neave, 1929; Claassen, 1931 (description of nymph, no illustrations); Hoppe, 1938; Gaufin, 1955; Jewett, 1959 and 1960 (male and female genitalia); Knight et al., 1965b (ova); Gaufin et al., 1966 (male and female genitalia, and adult head and pronotum); Newell, 1970; Baumann, 1971; Gaufin et al., 1972 (male and female genitalia, and adult head and pronotum); Stewart et al., 1974; Ricker and Scudder, 1975; Baumann et al., 1977 (male and female genitalia and adult head and pronotum). *Isoperla sobria,* Banks, 1907a.

Male. — Macropterous. Length of forewings 9-11 mm; length of body 8-11 mm. General body color medium to dark brown. Head-pronotal pigment pattern dark. Ocelli connected by triangular dark pigment, extending outward from anterior ocellus to antennal bases; wide bowl-shaped medium brown pigment band on back of head to lateral ocelli; interocellar space light; anterior frons with dark transverse band, connected posteriorly with ocellar-antennal band and enclosing triangular light spot; posterolateral margins of head with medium brown pigment and dark spots (Fig. 84). Pronotum with median yellow stripe, and dark brown rugosities (Fig. 84). Abdominal terga with 8 rows of longitudinal dots, 2 mesal, and 3 each laterally. Posterior margin of cercal segments with long ventral hair. Paraprocts very broad at base, tapering apically to acute, fine tips covered with small, fine hairs, and recurving slightly over 10th tergum (Figs. 90 & 91). Vesicle obsolescent. Aedeagus entirely membranous, tubular, apically expanded; expanded portion bearing transverse wide band of small, stout spinulae (Figs. 85B & 92B), interrupted at posterior margin by narrow vertical band of long hair-like spinulae (Figs. 85C & 92A); apex void of spinulae with 2 pointed lobes (Figs. 85D & 92C); proximal stalk covered with very small, dispersed spinulae (Fig. 85A).

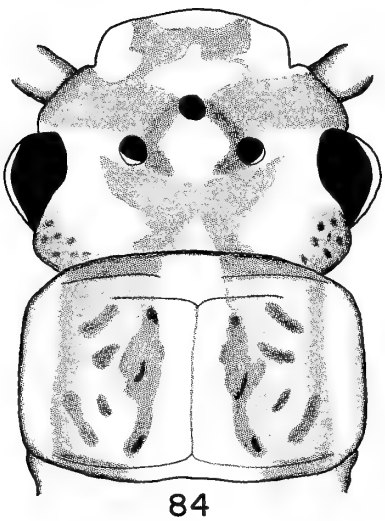
Female. — Macropterous. Length of forewings 11-13 mm; length of body 10-13 mm. General body color, and head-pronotal pigment pattern similar to male. Subgenital plate broad at base, produced posteriorly 1/4 length of 9th sternum, often broadly rounded posteriorly (Fig. 89) (sometimes truncate with shallow, median emargination). Vagina with narrow ventral band of small stout spinulae (Fig. 87A), and seminal receptacle (Fig. 87B) with 8 accessory receptacular glands (Fig. 87C).

Nymph (Reared). — Length of mature male nymph 10-11 mm; length of mature female nymph 12-14 mm. Dorsum of head with diamond-shaped narrow dark band, open at back, connecting ocelli; 2 circular lighter brown pigment bands enclosing light spots behind eyes; frons mostly brown except T-shaped light area and pair each of enclosed light bands and spots (Fig. 86). Laciniae with 2 large teeth; subapical tooth approximately 1/2 length of apical tooth, inner lacinial margin with row of 8-10 long stout hairs; row of irregular slender hairs below long stout hairs (Fig. 88). Pronotum with median yellow stripe, 2 wide longitudinal suffused brown bands with dark rugosities, and fringed with small setae (Fig. 86). Abdominal terga with paired longitudinal rows of light areas lateral to median, and 8 rows of longitudinal dots, 2 mesal, and 3 each laterally. Femora with scattered dorsal fringe of long fine hairs, tibiae with continuous dorsal fringe, and tarsi with few long dorsal hairs. Posterior margin of cercal segments with whorl of small, stout hairs, one long dorsal and ventral hair at posterior margin after 18th segment, continuous dorsal and ventral fringe after 21st segment.

Ova. — General shape oval, cross section circular (Fig. 93). Color medium brown. Length .29 mm; width .22 mm; collar well developed and expanded at apex, base with a depression void of chorionic sculpturing (Figs. 93, 94 & 96). Chorion evenly spaced small punctations, ridges barely evident (Figs. 93, 94 & 95). Micropyles undetected.

Material examined. — TYPES: *I. ebria,* Holotype ♀, *USA* — COLORADO: Colorado mountains, 1873, Collector ? (MCZ #248). *I. sobria,* Holotype ♀, *USA* — COLORADO: Colorado mountains, 1973, Collector ? (MCZ #247). Additional specimens — *CANADA* — ALBERTA: Maligne Lake, 21/VII/1925, F. Neave, 2 ♀ (INHS), Maligne Lake, 2/VII/1915, Collector ?, 1 ♂, 5 ♀ (CU), Banff, 18/VI/1925, O. Bryant, 1 ♂ (CU), Lake Louise, 4/VIII/1927, C. R. Crosby, 1 ♀ (CU). BRITISH COLUMBIA: Penticton, Shingle Crk., 19/IV/1935, A. N. G., 1 nymph (INHS), Penticton, Shingle Crk., 13/V/1935, A. N. G., 1 ♂, 1 exuvia (INHS). *USA* — CALIFORNIA: Nevada Co., Spring Trib. to Sagehen Crk., 11-12 & 31/VIII/1965, A. L. Sheldon, 4 ♂, 7 ♀, 16 nymphs (USNM), Sagehen Crk., 30/V/1966, A. L. Sheldon, 1 ♀ (USNM), Sagehen Crk., 13/IX/1965, A. L. Sheldon, 4 ♂, 1 ♀ (USNM); Siskiyou Co., Shasta, head of Sacremento Mt., 5/VI/1965, S. G. Jewett, 1 ♂, 2 ♀ (CU); Tuolumne Co., Yosemite National Park, Date ?, H. J. Raynor, 1 ♂, 2 ♀ (CU). COLORADO: Grand Co., Rocky Mt. National Park, Chasm Falls, 27/VII/1938, J. A. and H. H. Ross, 1 ♂, 2 ♀ (INHS), Rocky Mt. National Park, Fall R., 24/VII/1960, A. R. Gaufin, 1 ♀ (UU); Routt Co., Green Crk., 16/VII/1968, B. R. Oblad, 1 ♀ (UU); County ?, Independence Pass, Lake Crk., 6/VIII/1943, J. A. and H. H. Ross, 2 ♀ (INHS), Clairsden, Trib. of Smith Crk., 11/VI/1952, W. E. Ricker, 2 ♂, 3 ♀ (WR). MONTANA: Gallatin Co., Locality ?, 15/VII/1913, Collector ?, 1 ♀ (CU), Hyalite Crk., 13/VI/1951, R. Hays, 1 ♂, 3 exuviae (UU); Glacier Co., Glacier National Park, below Red Rock Lake, Swift Current Crk., 18/VII/1966, A. R. Gaufin, 1 ♀ (RWB), Trib. of Wilber Crk., 19/VII/1966, J. L. Miner, 1 ♀ (RWB), Many Glacier Area, Lake Josephine, 9/VIII/1966, A. R. Gaufin, 1 ♀ (RWB), Glacier National Park, Many Glacier Area, Lower Area D, 21/VIII/1966, A. R. Gaufin, 1 ♀ (UU), Glacier National Park, Elizabeth Crk., 10/VII/1970, C. M. Yarmoloy, 1 ♂, 1 ♀ (UU); Park Co., 1/2 mi. above Hwy. 212, Island Lake, 28/VII/1966, J. R. Grierson, 1 ♂ (UU), above W. Fork of Bitterroot R., Trapper Crk., 30/VI/1965, J. R. Grierson, 1 ♂ (UU), S. of Darby, Hwy. 93, Fern Crk., 18/VI/1965, A. R. Gaufin, 1 ♀ (UU). NEW MEXICO: Santa Fe Co., Big Tesuque Campground, Big Tesuque

FIGURES 84-92. — *I. sobria.* 84. adult head and pronotum (scale: 1 mm = .05 mm). 85. male aedeagus, posterior aspect, A. proximal tube with very small scattered spinulae, B. transverse, wide band of concentrated small stout spinulae, C. mesoposterior band of long hair-like spinulae, D. apical pointed lobe (1 mm = .04 mm). 86. nymph head and pronotum (1 mm = .08 mm). 87. female vagina, A. vaginal armature, B. seminal receptacle, C. receptacular duct, D. accessory receptacular glands, E. subgenital plate (1 mm = .02 mm). 88. nymphal maxilla, A. stipe, B. lacinia, C. apical tooth, D. galea, E. maxillary palpus (1 mm = .04 mm). 89. female subgenital plate (1 mm = .09 mm). 90. male paraproct, lateral aspect (1 mm = .02 mm). 91. male paraproct, dorsal aspect (1 mm = .02 mm). 92, male aedeagus, lateral aspect, A. mesal posterior band of long hair-like spinulae, B. transverse, wide band of concentrated small stout spinulae, C. apical pointed lobe (1 mm = .04 mm).



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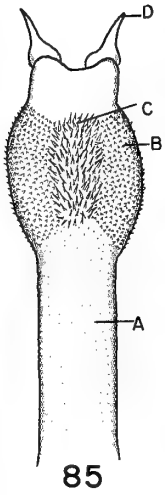

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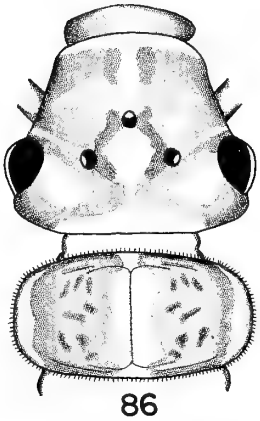

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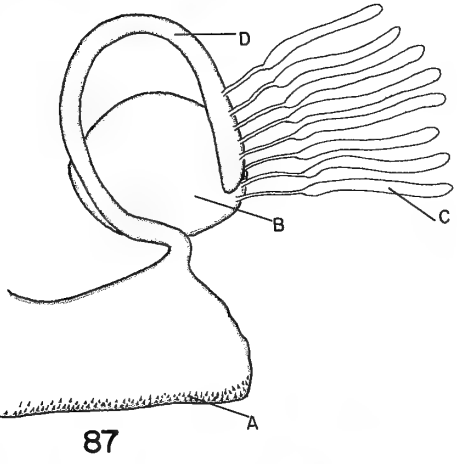

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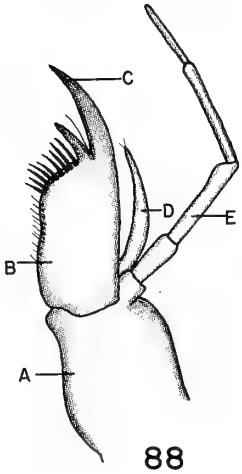

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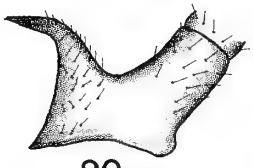

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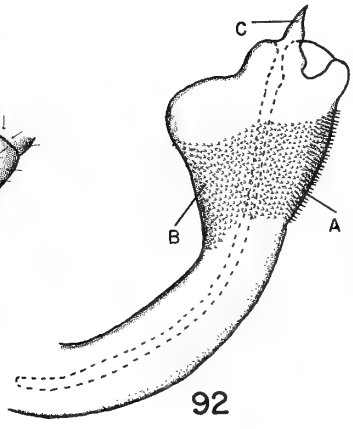

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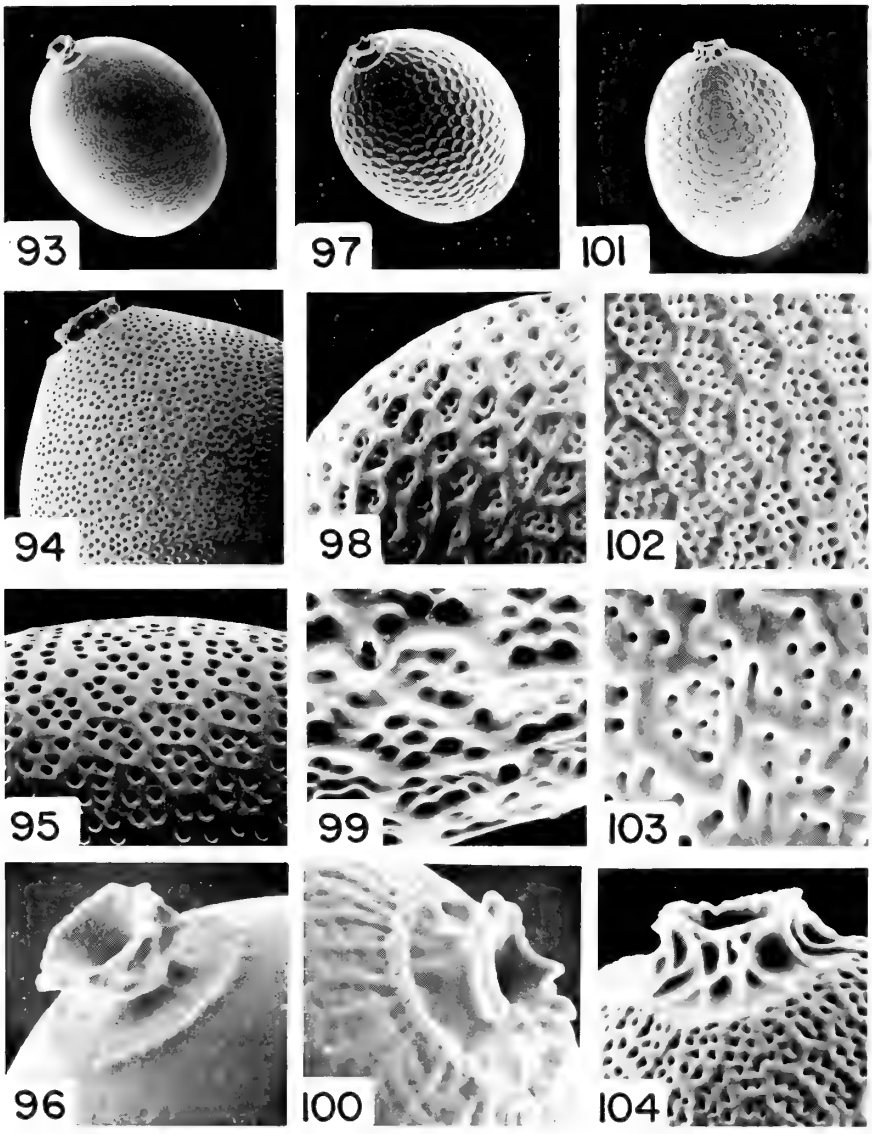


FIGURES 93-104. — Figs. 93-96. *I. sobria.* 93. whole ova 200×. 94. detail anterior 1/2 400×. 95. detail of chorion 1000×. 96. detail of collar 1000×: Figs. 97-100. *I. gravitans.* 97. whole ova 200×. 98. detail of chorion 700×. 99. detail of micropyles 200×. 100. detail of collar 1000×: Figs. 101-104. *I. tilasqua.* 101. whole ova 200×. 102. detail of chorion 1000×. 103. detail of micropyles 2000×. 104. detail of collar 1000×.

Magnifications represent original values before reduction of plates.

Crk., 10/VI/1974, B. P. Stark and T. A. Wolff, 1 ♂ (BS); Taos Co., Rio Trampos, 20/IV/1973, B. P. Stark and T. A. Wolff, 1 nymph (BS). OREGON: Benton Co., Muddy Crk., 12/IV/1938, S. G. Jewett, 4 nymphs (SGJ); Clackamas Co., Mollala R., 13/VI/1938, S. G. Jewett, 1 ♀ (INHS); Deschutes Co., Fall R., 13/VII/1948, S. G. Jewett, 4 ♂, 17 ♀ (UU), Fall R., 7/VI/1949, S. G. Jewett, 1 nymph (SJ); Hood R. Co., Hood R. Meadows, 10/VIII/1955, S. G. Jewett, 1 ♂, 1 ♀ (UU); Klamath Co., Crater National Park, Annie Crk., 24/VI/1956, J. Schuh, 2 ♂, 2 ♀ (OSU[2]), Collier State Park, 21/IV/1951, S. G. Jewett, 11 ♂, 18 ♀ (UU), Cherry Crk., 26/VI/1937, S. G. Jewett, 1 ♀ (INHS), Upper Klamath R., Denny Crk., 19/V/1952, S. G. Jewett, 4 ♂, 3 ♀ (SJ). UTAH: Salt Lake Co., Brighton, Big Cottonwood Crk., 6/IV/1954, A. R. Gaufin, 4 ♀, 35 nymphs (UU), Brighton, Big Cottonwood Crk., 15/V/1954, A. R. Gaufin, 17 nymphs (UU), Lambs Canyon Crk., 26/V/1965, R. W. Baumann, 6 nymphs (RWB), Pinecrest, Emigration Canyon, 26/IX/1966, R. W. Baumann, 4 nymphs (RWB); Uintah Co., Roosevelt, Cottonwood Crk., 15/VI/1936, F. C. Harmston, 2 ♂ (INHS); Wasatch Co., Trout Crk., 30/VI/1965, D. C. Hales, 1 ♂ (UU), Trout Crk., 18/III/1966, D. C. Hales, 1 nymph (UU). WYOMING: Albany Co., Centennial, 2/VII/1938, D. J. and J. N. Knull, 1 ♂ (INHS), Gold Nesh Fork Crk., 23/VII/1972, W. E. Ricker, 1 ♀, 1 nymph (SJ), Foxpark, 4/VII/1938, Collector ?, 2 ♀ (UU); Park Co., above Hwy. 212, Beartooth Crk., 28/VII/1966, J. R. Grierson, 1 ♂ (RWB), 7 mi. E. of Mammoth Hot Springs, Blacktail Deer Crk., 26/VI/1964, J. W. Richardson and S. L. Jensen, 1 ♂ (RWB).

Distribution. — CANADA: Alberta, British Columbia; USA: Alaska, Arizona, California, Colorado, Idaho, Montana, New Mexico, Oregon, Utah, Washington, and Wyoming (Fig. 83).

Diagnosis and Discussion. — *I. sobria* is most similar to *I. tilasqua.* Males can be distinguished by the absence of a vesicle on the 8th sternum, longer, thinner, more acute paraprocts, aedeagus bearing only one posterior patch of long, hair-like spinulae, 2 pointed dorsal lobes, apex void of spinulae, and narrower patch of small stout spinulae. Females can be differentiated by the broadly rounded subgenital plate void of small hairs. The nymph of *I. tilasqua* is unknown. Ova can be distinguished from those of *I. tilasqua* by the lower chorionic ridges, and depressed area void of sculpturing at base of the collar.

I. ebria (Hagen) is placed in synonymy with *I. sobria* (Hagen) based on a direct comparison of the type specimens and scanning electron microscope study of the ova. The type specimen of *I. ebria* exhibited a broadly rounded subgenital plate but in the type of *I. sobria* there was a median emargination. This variation was noted in many of the *I. sobria* populations examined. The ova from both types were identical, and no variation in aedeagal characters was observed over the geographic range of *I. sobria.*

Dodds and Hisaw (1925) reported that *I. ebria* was distributed between 5,500-11,000 feet in the Colorado Rockies. No studies on the life

history or general biology have been done. Material examined indicated emergence occurs in mid-May to early Aug., with largest numbers collected early-Jul. Nymphs are found in creeks and small- to medium-sized rivers.

Isoperla gravitans (Needham and Claassen)

Clioperla gravitans, Needham and Claassen, 1925, 2:138. Holotype ♂: Olympia, Thurston Co., Washington, USA, (CU-Type is missing), (wings and male genitalia).

Isoperla gravitans, Hoppe, 1938, 4:156.

Clioperla gravitans, Claassen, 1940, 232:196.

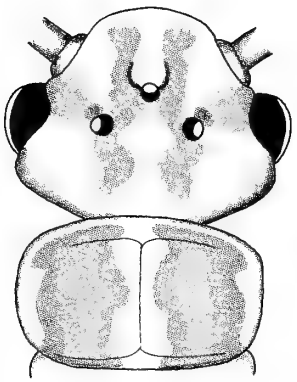
Isoperla gravitans, Jewett, 1954, 11:548. Allotype ♀: Youngs R., Clatsop Co., Oregon, USA, 1/V/1940, S. G. Jewett (CAS), (female genitalia).

Isoperla gravitans, Illies, 1960:405.

Additional references: *Isoperla gravitans,* Jewett, 1959, (male and female genitalia).

Male. — Macropterous. Length of forewings 14-16 mm; length of body 12-15 mm. General body color medium brown. Head pattern consisting of dark "H"-shaped mark in center, and lighter brown transverse bar across frons between eyes (Fig. 105). Pronotum with median yellow stripe; discs with wide longitudinal medium brown pigment band and vermiculate markings (Fig. 105). Forewings light, veins dark brown. Femora, tibiae and tarsi dark brown; femora with light yellow band at distal end. Abdominal terga with 8 faint rows of longitudinal dots, 2 mesal and 3 each laterally. Cerci dark brown, bearing small fine hairs. Paraprocts short, stout, tapering to blunt points apically, broad at base, appearing triangular from above, recurving anteriorly barely over 10th tergum, and bearing medium fine hairs (Fig. 107 & 108). Vesicle, very broad at base, rounded at apex, much lighter than rest of segment (Fig. 106). Ninth sternum and tergum much lighter than rest of abdominal segments. Aedeagus entirely membranous, tubular, apex expanded into large rounded lobe void of spinulae; small nipple at anterodorsal margin, large posteromesal lobe with "T"-shaped band of medium length spinulae and 2 spinulae free patches posteriorly (Figs. 109B & 110D); band of scattered fine spinulae encircling mesal section, interrupted before posteromesal lobe (Figs. 109D & 110C), wide band of small stout spinulae encircling aedeagus below posteromesal lobe (Figs. 109C & 110B), small patch of medium-length stout spinulae at posteroventral margin (Figs. 109A & 110A).

FIGURES 105-111. — *I. gravitans.* 105. adult head and pronotum (scale: 1 mm = .08 mm). 106. male vesicle and 8th sternum (1 mm = .07 mm). 107. male paraproct, lateral aspect (1 mm = .02 mm). 108. male paraproct, dorsal aspect (1 mm = .02 mm). 109. male aedeagus, lateral aspect, A. posteroventral patch of medium-length stout spinulae, B. posteromesal lobe with "F"-shaped band of medium length spinulae, C. wide band of small stout spinulae, D. mesal band of scattered fine spinulae (1 mm = .04 mm). 110. male aedeagus, posterior aspect, A. posteroventral patch of medium-length stout spinulae, B. wide band of small stout spinulae, C. mesal band of scattered fine spinulae, D. posteromesal lobe with "T"-shaped stout spinulae (1 mm = .04 mm). 111. female subgenital plate (1 mm = .03 mm).



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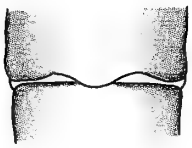

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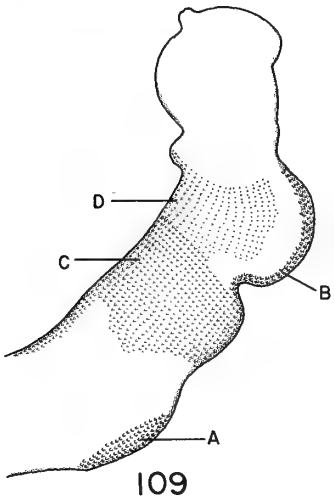

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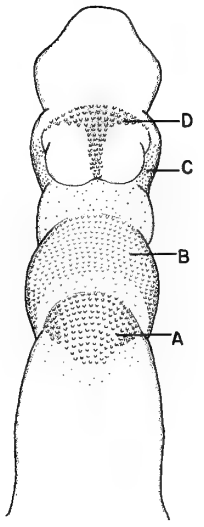

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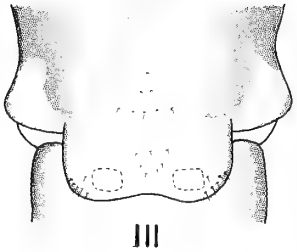

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Female. — Macropterous. Length of forewings 16-20 mm; length of body 15-18 mm. General body color and head-pronotal pigment pattern similar to male. Subgenital plate truncate, lateral margins parallel with sides of abdomen, shallow median emargination at posterior margin; produced 2/3 length over 9th sternum; 2 sclerotized patches on inner surface at posterolateral margins, lighter than rest of segment; light pigmentation extending to base of 8th sternum forming "V"-shaped pattern (Fig. 111). Ninth and 10th abdominal segments lighter than rest.

Nymph. — Unknown.

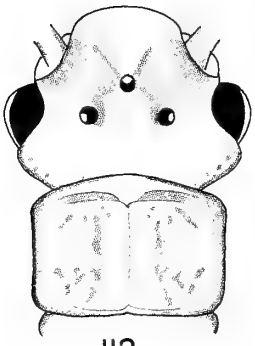
Ova. — General shape oval, cross section circular (Fig. 97), color medium brown. Length .30 mm; width .24 mm. Collar well developed and expanded apically (Figs. 97 & 100). Chorionic ridges elevated forming distinct hexagonal depressions bearing 4-7 evenly spaced punctations (Figs. 97-100). Micropyles arranged in pairs on top of ridges near bottom 1/3 on one side (Fig. 99).

Material examined. — *USA* — OREGON: Benton Co., Oak Crk., 17&19/V/1968, C. D. Kerst, 1 ♂, 5 ♀ (RWB), Oak Crk., 18/IV/1935, R. Dimick, 2 ♀ (WR), Oak Crk., 16/V/1969, C. D. Kerst, 1 ♂ (USNM), Oak Crk., 10/V/1969, C. D. Kerst, 1 ♂, 1 ♀ (SJ), Oak Crk., 7/V/1969, C. D. Kerst, 1 ♂, 3 ♀ (USNM); Clackamas Co., Mt. Hood, Still Crk. Campground, 17/VI/1967, S. G. Jewett, 2 ♀ (USNM); Clatsop Co., 2 mi. E. of Elsie, Osweg Crk., 3/V/1964, S. G. Jewett, 1 ♂ (SJ), 4 mi. N.E. of Elsie, at Red Bluff, Nehalem R., 10&11/V/1965, S. G. Jewett, 1 ♂, 2 ♀ (RWB); Columbia Co., Clatskanie, Beaver R., 9/V/1936, J. Schuh, 1 ♂, 4 ♀ (WR). WASHINGTON: Clark Co., Ellsworth, 14/VI/1941, S. G. Jewett, 2 ♂ (SJ), Ellsworth, 27/III/1941, S. G. Jewett, 1 ♀ (SJ), Ellsworth, 1/IV/1941, S. G. Jewett, 1 ♂ (WR); King Co., Fall City, Raging R., 30/IV/1932, G. N. Hoppe, 1 ♂ (WR).

Distribution. — USA: Oregon and Washington (Fig. 83).

Diagnosis and Discussion. — *I. gravitans* is most similar to *I. tilasqua.* Males can be distinguished by the wide, longitudinal, medium brown bands on pronotum, light yellow vesicle, light yellow 9th and 10th abdominal segments, stouter paraprocts, absence of 2 long narrow apical lobes, and 2 posterior patches of long hair-like spinulae on aedeagus. Females can be separated by the pigment patterns mentioned above, lighter pigmentation of the subgenital plate, presence of 2 sclerotized patches on inner

FIGURES 112-117. — *I. tilasqua.* 112. adult head and pronotum (scale: 1 mm = .08 mm). 113. male vesicle and 8th sternum (1 mm = .08 mm). 114. male paraproct, lateral aspect (1 mm = .03 mm). 115. male aedeagus, posterior aspect, A. posteroventral lobe bearing patch bearing long hair-like spinulae, B. wide band of small stout spinulae, C. constricted section bearing concentrated small stout spinulae, D. narrow posterior band of long, hair-like spinulae, E. expanded apex with scattered small fine spinulae (1 mm = .05 mm). 116. male aedeagus, lateral aspect, A. posteroventral band of long hair-like spinulae, B. wide band of small stout spinulae, C. constricted section bearing concentrated small stout spinulae, D. narrow posterior band of long, hair-like spinulae, E. expanded apex with scattered small fine spinulae, F. dorsal tubular processes (1 mm = .04 mm). 117. female subgenital plate (1 mm = .02 mm).



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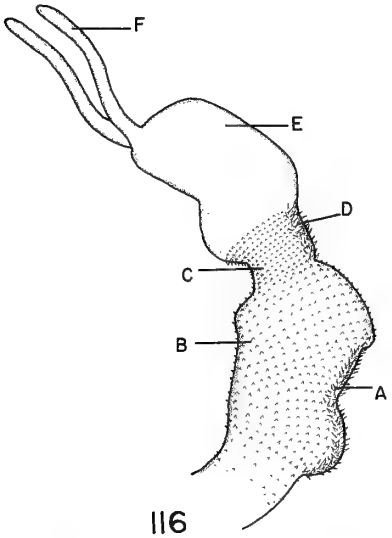

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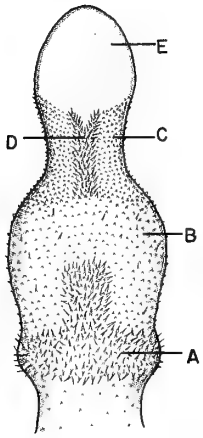

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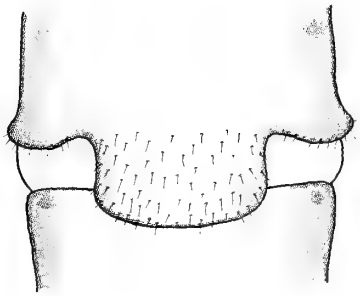

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surface at posterolateral margins, and light 9th and 10th abdominal segments. Ova can be differentiated by the thicker chorionic ridges, larger size, fewer punctations in each depression, and the absence of a small groove preceding each micropyle opening.

Needham and Claassen (1925) described this species from a single male specimen, and indicated that it was in the Cornell University collection, although Cornell has no record of it ever being received or deposited.

No life history or general biology data are available for this species. Based on the material examined, emergence occurs early Apr. to mid-Jun., with largest numbers collected mid-May. Nymphs are found in creeks and small rivers.

Isoperla tilasqua NEW SPECIES

Male. — Macropterous. Length of forewings 10-12 mm; length of body 11-12 mm. General body color dark brown. Head-pigment pattern dark. Lateral ocelli connected to anterior ocellus by a dark brown inverted "U"-shaped band; interocellar space light; arms of the inverted "U"-band connected to back margin of head by progressively diminishing vermiform brown pigmentation; 2 large ovate dark brown spots connecting anterior ocellus to base of antennae; pair of club-shaped marks extending from these spots onto anterior frons (Fig. 112). Pronotum mostly light brown, with median light stripe, dark brown lateral rugosities and anterior transverse dark band (Fig. 112). Abdominal terga with 8 rows of longitudinal dots, 2 mesal, and 3 each laterally. Posterior margin of each cercal segment with long ventral hair. Paraprocts short, stout, tapering to points apically, bearing small fine hairs, and recurving forward to level of 10th tergum (Fig. 114). Vesicle, broad at base, rounded at apex, and darker than rest of segment (Fig. 113). Aedeagus entirely membranous, tubular and constricted near middle; 2 long narrow tubular lobes apically (Fig. 116F); one posteroventral lobe bearing long hair-like spinulae patch which extends into a longitudinal band (Figs. 115 & 116A); constricted section bearing concentrated patch of small, fine spinulae (Figs. 52, 53, 115 & 116C), and narrow posterior band of long hair-like spinulae bifurcated at apex (Figs. 53, 115 & 116), dorsum expanded bearing scattered small fine spinulae (Figs. 115 & 116D); proximal 1/2 bearing small stout spinulae (Figs. 51, 115 & 116B).

Female. — Macropterous. Length of forewings 13-16 mm; length of body 15-17 mm. General body color, and head-pronotal pigment pattern similar to male. Subgenital plate truncate, lateral margins parallel with sides of abdomen, produced posteriorly 1/4 length of 9th sternum, bearing scattered fine hairs (Fig. 117).

Nymph. — Unknown.

Ova. — General shape oval, cross section circular (Fig. 101). Color light brown. Length .28 mm; width .21 mm. Collar well developed with outer partitioned projections (Figs. 101 & 104). Chorionic ridges raised forming distinct hexagonal depressions with 8-14 evenly spaced small punctations (Fig. 101-104). Micropyles with a small groove preceding each opening, and arranged in pairs on top of ridges near bottom 1/2 on one side (Fig. 103).

Material examined. — TYPES: Holotype ♂, *USA* — OREGON: Benton Co., Trap 1, Oak Crk., 13/VI/1968, C. D. Kerst (USNM); allotype ♀, *USA* — OREGON: Benton Co., Trap 2, Oak Crk., 22/V/1969, C. D. Kerst (USNM). Paratypes, OREGON: Benton Co., Trap 2, Oak Crk., 19-22/VI/1968, C. D. Kerst, 1 ♀ (USNM), Trap 1, Oak Crk., 16-18/V/1969, C. D. Kerst, 1 ♂ (USNM); Clackamas Co., Mt. Hood, Still Crk. Campground, 17/VI/1967, S. G. Jewett, 2 ♀ (USNM); Clatsop Co., Big Crk., 9/V/1947, S. G. Jewett, 1 ♂ (SJ); Columbia Co., Keasy, Rock Crk., 23/V/1954, S. G. Jewett, 1 ♀ (SJ); Klamath Co., Spring Crk., 8/V/1967, J. Schuh, 2 ♀ (USNM); Lane Co., Fern Ridge Res., 1/V/1946, S. G. Jewett, 1 ♀ (SJ), (Paratypes deposited at USNM, SJ, SWS & NTSU).

Distribution. — USA: Oregon (Fig. 83).

Diagnosis and Discussion. — *I. tilasqua* is most clearly allied with *I. sobria* based on male and female genital characters and pigment patterns (see diagnosis under *I. sobria*). Ova are more similar to *I. gravitans,* having well-developed chorionic ridges and distinct hexagonal-shaped depressions with many evenly spaced punctations.

This species is found in small- to medium-sized creeks and is limited to the Coastal and Cascade Mountain Ranges in Oregon (Fig. 83). Emergence begins in early May and continues until mid-Jun.

Etymology. — The name "tilasqua" was taken from the Indian name for big creek. The first specimen of this species examined was from Big Creek, in Clatsop County, Oregon.

SPECIES GROUP D

Isoperla marmorata complex

This group is composed of *I. fulva* Claassen and *I. marmorata* (Needham and Claassen). They share the following characteristics: 1. male aedeagus bearing a spinose, club-shaped, sclerotized process; 2. broadly rounded, shallow male vesicle; 3. broad variable-shaped subgenital plate, often angulate; 4. nymphal head pattern with interocellar space, frons and clypeus mostly dark brown; 5. two wide longitudinal concolorous dark brown bands with no rugosities on nymphal pronotum; 6. dorsal fringe of long fine hairs on nymphal tibiae and tarsi; 7. 2 wide dark brown lateral stripes and one narrow median light brown stripe on nymphal abdominal terga; and 8. ova with developed collar and elevated thickened chorionic ridges forming distinct hexagonal depressions with evenly spaced small punctations.

I. marmorata is mainly restricted to the Coastal, Cascade, and Olympic mountain ranges along the Pacific Coast, and occurs in small creeks to medium-sized rivers. *I. fulva* has a broad distribution from the Southern, Central and Northern Rocky Mountains to the Pacific Coast (Fig. 118),

and inhabits creeks and rivers of all sizes. Emergence occurs from early May in southern latitudes until Aug. in the north; both species are thought to undergo univoltine life cycles.

Isoperla marmorata (Needham and Claassen)

Clioperla marmorata, Needham and Claassen, 1925, 2:142. Holotype ♀; Reno, Washoe Co., Nevada, USA (CU #1,166), (wings and female genitalia).
Clioperla marmorata, Claassen, 1940, 232:196.
Isoperla marmorata, Jewett, 1954b, 30:178. Allotype ♂; Eagle Crk., Clackamas Co., Oregon, USA (CAS), (male genitalia).
Isoperla marmorata, Illies, 1966:409.

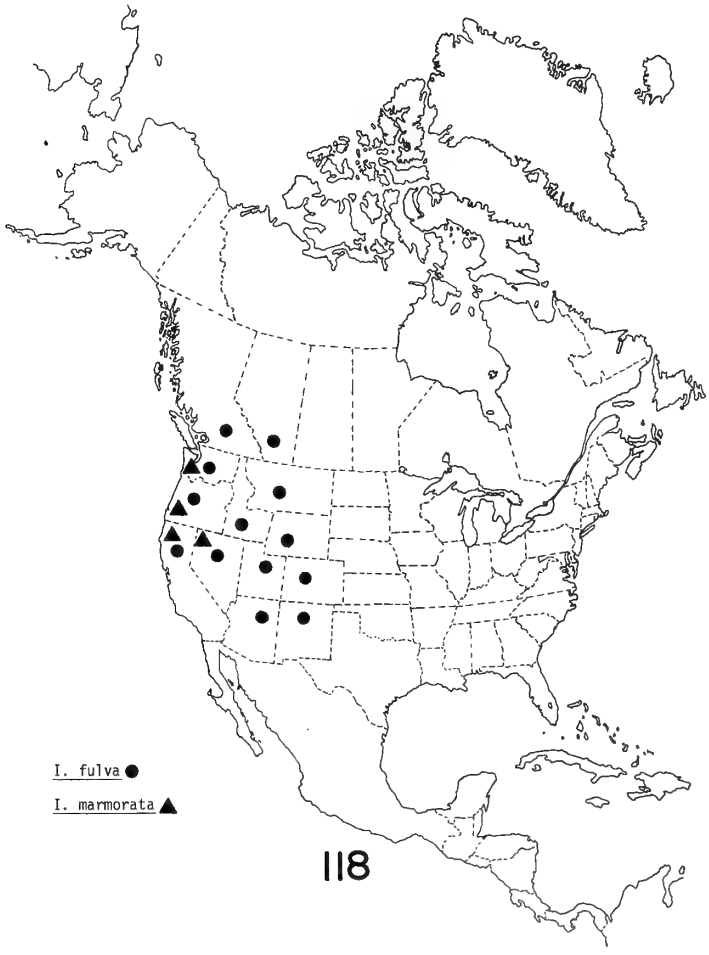


FIGURE 118. — Distribution of the *I. marmorata* complex.

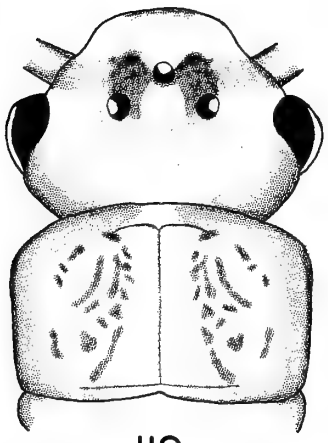
Additional references: *Isoperla marmorata*, Jewett, 1956, 1959 and 1960 (wings and male genitalia); Sheldon and Jewett, 1967; Kerst and Anderson, 1974 and 1975.

Male. — Macropterous. Length of forewings 9-11 mm; length of body 9-11 mm. General body color medium brown. Ocelli of head connected by distinct dark brown "M"-shaped pigment pattern; interocellar space light yellow; light brown pigment band extending across top "M"-band between antennal bases; wide median light brown band on anterior frons, and light brown, variable patch of pigmentation connecting lateral ocelli; large brown patch behind each eye (Fig. 119). Pronotum light brown with median yellow stripe and small vermiform dark brown rugosities (Fig. 119). Wings hyaline, veins light brown, anal area of hind wings fumose. Femora, tibiae, and tarsi medium brown, femora with yellow band at distal end. Abdominal terga with 8 faint rows of longitudinal dots, 2 mesal, and 3 each laterally. Paraprocts wide at base, tapering to long fine points apically, bearing scattered small fine hairs (Fig. 122). Cerci with one long ventral hair at posterior margin; anterior 1/4 of each segment lighter than remainder. Vesicle shallow, broadly rounded, darker than rest of segment (Fig. 121). Aedeagus capitate; expanded apex bearing scattered, large rounded spinulae (Fig. 123F) and median nipple void of spinulae (Fig. 123G); posterior margin with thin sclerotized process appearing clavate laterally and bearing a row of small spines dorsally and ventrally on expanded portion (Fig. 123D); patch of large stout spines above insertion of process (Fig. 123E); small nipple below sclerotized process void of spinulae (Fig. 123C); mesal constricted section, bearing a dense wide band of small, stout spinulae (Fig. 123H); expanded, basal lobe covered with scattered, small spinulae (Fig. 123B); proximal stalk bearing scattered, small, fine, hair-like spinulae (Fig. 123A).

Female. — Macropterous. Length of forewings 11-13 mm; length of body 10-13 mm. General body color and head-pronotal pigment patterns similar to male. Subgenital plate of 8th sternum reduced, barely produced over anterior margin of 9th sternum, broadly rounded at posterior margin (Fig. 124).

Nymph (Reared). — Length of mature male nymph 9-10 mm; length of mature female nymph 11-13 mm. Dorsum of head with 3 light yellow patches, one anterior to forward ocellus, and 2 between compound eyes and lateral ocelli. Interocellar space dark; occipital ridge of spinulae absent (Fig. 120). Pronotum with median yellow stripe separating 2 wide, dark brown lateral longitudinal bands; each band partially enclosing variable patch of yellow; margin fringed with evenly spaced small stout setae, occasional long setae interspersed at upper and lower angles (Fig. 120). Meso- and metanota with 2 wide lateral and 2 thin mesal dark brown longitudinal stripes. Femora with stout spine-like setae on dorsal margin, and interspersed on outer surface; tibia with dorsal fringe of long, fine hairs, tarsi with few scattered, dorsal, fine hairs. Abdominal terga with 3 longitudinal stripes, 2 wide, dark brown lateral stripes, and one narrow, median, light brown stripe. Posterior margin of cercal segments with whorl of small stout setae, one medium-length ventral hair at posterior margin each segment after 13th.

Ova. — General shape oval, cross section circular (Fig. 125). Color medium brown. Length .30 mm; width .20 mm. Collar developed and expanded slightly at apex with outer partitions (Figs. 125 & 126). Chorion with elevated thickened ridges forming hexagonal-shaped depressions bearing 9-14 evenly spaced punctations (Figs. 125-127). Micropyles arranged in pairs on top of ridges near bottom 1/3 on one side (Fig. 127).



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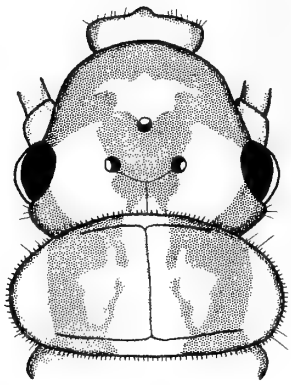

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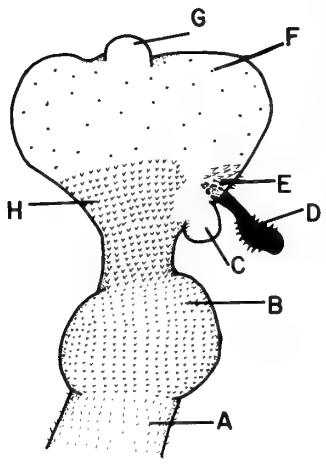

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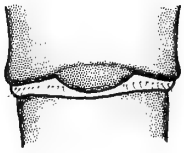

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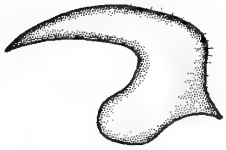

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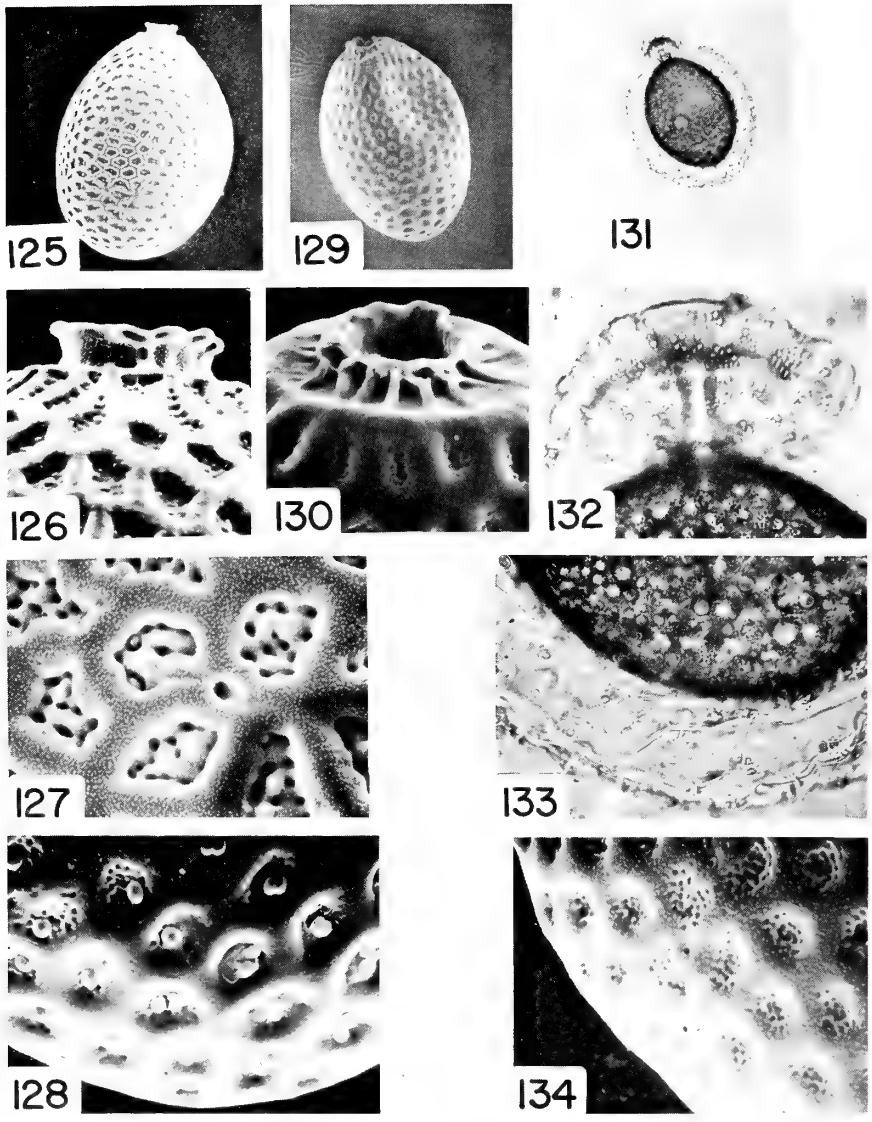
FIGURES 119-124. — *I. marmorata.* 119. adult head and pronotum (scale: 1 mm = .03 mm). 120. nymph head and pronotum (1 mm = .03 mm). 121. male vesicle and 8th sternum (1 mm = .05 mm). 122. male paraproct, lateral aspect (1 mm = .01 mm). 123. male aedeagus, lateral aspect, A. proximal stalk bearing scattered, small, fine, hair-like spinulae, B. expanded basal lobe bearing scattered small spinulae, C. small mesoposterior nipple-like lobe, D. sclerotized process, E. patch of large stout spines, F. expanded apex bearing scattered, large rounded spinulae, G. mesodorsal nipple, H. mesal band of dense small, stout spinulae (1 mm = .03 mm). 124. female subgenital plate (1 mm = .06 mm).

Material examined. — TYPES: Holotype ♀, NEVADA: Washoe Co., Reno, 1878, Morrison (CU #1,166). Allotype ♂, OREGON: Clackamas Co., Eagle Crk., 16/IV/1940, S. G. Jewett (CAS). Additional specimens — *USA* — CALIFORNIA: Butte Co., Chico, Richardson Springs, 5/IV/1962, S. G. Jewett, 6 ♂, 9 ♀, 7 exuviae (SJ); Fresno, 10 mi. N.E. of Academy, Dry Crk., 10/IV/1955, D. L. Abell, 2 ♂, 1 ♀ (SJ); Plumas Co., Grayeagle Crk., 8/VI/1965, S. G. Jewett, 4 ♂ (RWB). OREGON: Benton Co., Fisheries Lab, Oak Crk., 28/V/1977, S. W. Szczytko and K. W. Stewart, 1 ♀ (SWS & NTSU), Tampluko, 9 mi. N.W. of Corvallis, Berry Crk., 28/V/1977, S. W. Szczytko and K. W. Stewart, 1 ♀, 1 exuvia, 3 nymphs (SWS & NTSU); Corvallis, Oak Crk., 22/IV/1969, C. D. Kerst, 1 ♂ (SJ), Corvallis, Site 2, Oak Crk., 22/V/1969, C. D. Kerst, 3 ♀ (OS²), 9 mi. N.W. of Corvallis at Blacklight, Berry Crk., 20/VI/1968, C. D. Kerst, 1 ♀, (OS²), 4 mi. W. of Philomath, 27/IV/1963, J. Schuh, 1 ♀ (USNM), Philomath, Woods Crk., 15/V/1936, V. E. Starr, 1 ♀ (WR), Corvallis, Site 2, Oak Crk., 10/V/1969, C. D. Kerst, 7 ♀ (OS²); Clackamas Co., Eagle Crk., 16/VI/1940, S. G. Jewett, 4 ♂, 1 ♀ (SJ), Eagle Crk., 5/V/1940, S. G. Jewett, 3 ♂, 3 ♀ (LCMNH); Clatsop Co., Red Bluff, Nehalem R., 25/VI/1965, S. G. Jewett, 1 ♂, 1 ♀ (RWB), Klatskanine R., 12/VI/1948, S. G. Jewett, 1 ♂ (SJ); Columbia Co., Beaver Crk., 17/IV/1954, S. G. Jewett, 1 ♂ (UU), Keasy, Rock Crk., 23/V/1954, S. G. Jewett, 1 ♂ (RWB); Washington Co., near Timber Junct., Wolf Crk., 1/VII/1967, S. G. Jewett, 1 ♂, 5 ♀ (INHS). WASHINGTON: Grays Harbor Co., Upper Wynoochie R., 29/V/1977, S. W. Szczytko and K. W. Stewart, 3 ♂, 3 ♀, 3 exuviae (SWS & NTSU).

Distribution. — USA: California, Nevada, Oregon and Washington (Fig. 118).

Diagnosis and Discussion. — This species is similar to *I. fulva.* Males can be distinguished by the lighter pigment patterns of the head pronotum, fumose anal area of hindwings, longer more acute paraprocts, and the following aedeagal characters: 1. general capitate shape; 2. clavate shape and dorsal-ventral spinulation of sclerotized process; 3. expanded, spinulated large lobe beneath constricted mesal section; 4. proximal stalk with scattered, small fine hair-like spinulae; and 5. absence of 2 long anterior tubular lobes. Females can be differentiated by the lighter pigment patterns of the head and pronotum, fumose anal area of hindwings, and often by the more shallow subgenital plate (in several specimens of *I. fulva* from Utah and Montana the shape of the subgenital plate is very similar). Nymphs can be separated by the lack of occipital spinulae, medium-length ventral hair at posterior margin of cercal segments after 12th segment, and 4 dark brown longitudinal stripes on meso- and metanota. Ova can be separated by the larger size, thinner chorionic ridges, and larger punctations.

Sheldon and Jewett (1967) reported that *I. marmorata* was a rare stonefly in the fauna of a Sierra Nevada stream emerging in early June. Kerst and Anderson (1974) found that emergence extended from late



FIGURES 125-134. — Figs. 125-127. *I. marmorata.* 125. whole ova 200×. 126. detail of crown 1000×. 127. detail of chorion and micropyle 2000×: Figs. 128-134. *I. fulva.* 128. detail of chorion with proteinaceous bodies 1000×. 129. whole ova 200×. 130. detail of collar 1000×. 131. light micrograph of whole ova with enveloping gelatinous membrane 80×. 132. light micrograph — detail of collar and enveloping gelatinous membrane 800×. 133. light micrograph — detail of gela-

May until late July in Oak Crk., Benton Co., Oregon. Material examined in this study emerged from early Apr. until mid-Jun., beginning in southern latitudes and lower altitudes.

This is apparently a rare species and no studies have been done on its life history or general biology.

Isoperla fulva Claassen

Isoperla fulva, Claassen, 1937, 69:80. Holotype ♂, and allotype ♀; Logan R., Cache Co., Utah, USA (CU #1,687), (adult head and pronotum, male and female genitalia).

Isoperla chrysannula, Hoppe, 1938, 4:156. Holotype ♂, Shelton, Washington, USA (TBM); (male genitalia). Syn. Frison, 1942.

Isoperla cascadensis, Hoppe, 1938, 4:158. Holotype ♂, and allotype ♀, Tokul Crk., Washington, USA (TBM); (male and female genitalia). Syn. Frison, 1942.

Isoperla fulva, Claassen, 1940, 232:200.

Isoperla fulva, Frison, 1942, 22:337. Syn. indicated.

Isoperla fulva, Illies, 1966:403.

Isoperla fulva, Zwick, 1973:245.

Additional references: *Isoperla fulva,* Knowlton and Harmston, 1938; Ricker, 1939, 1943 (nymphal description, habitus female nymph, and maxilla); Gaufin, 1955; Jewett, 1959, 1960 (male and female genitalia); Knight and Gaufin, 1965, Knight et al., 1965a (ova); Knight and Gaufin, 1966, Nebeker and Gaufin, 1966, Gaufin et al., 1966 (adult mesosternum, wings, male and female genitalia and aedeagus); Knight and Gaufin, 1967; Newell, 1970; Richardson and Gaufin, 1971; Baumann, 1971; Gaufin et al., 1972 (wings, male and female genitalia); Stewart et al., 1974, Ricker and Scudder, 1975; Baumann et al., 1977 (adult mesosternum, ova, wings, male and female genitalia, and aedeagus); Fuller and Stewart, 1977.

Male. — Macropterous. Length of forewings 8-9 mm; length of body 8-9 mm. General body color medium to light brown. Ocelli of head and bases of antennae connected by dark brown "M"-shaped pigment band; median, quadrangular light brown spot behind lateral ocelli; interocellar space light (Fig. 135). Pronotum light brown, median yellow stripe, rugosities dark brown (Fig. 135). Wings fumose, veins medium brown. Femora, tibiae and tarsi medium brown. Abdominal terga with 8 faint rows of longitudinal dots, 2 mesal and 3 each laterally. Paraprocts short, stubby, not recurving over 10th tergum (Figs. 140 & 142). Cerci with long ventral hair at posterior margin of each segment, one medium-length dorsal hair at posterior margin of segments 1-11. Vesicle shallow, broadly rounded, darker than rest of segment (Fig. 136). Aedeagus with large conical, posterodorsal lobe of small stout spinulae bearing clavate (lateral view) apical sclerotized process; tips of process pale, ladle-shaped, bearing long, stout spinulae (Fig. 138F); patch of long, stout spinulae anterior to process insertion (Fig. 138E); anterodorsal portion of aedeagus with large conical lobe void of spinulae (Fig. 138D); 2 long, narrow, membranous tubular

tinous membrane at posterior end 800×. 134. detail of chorion and micropyles 1000×.

Magnifications represent original values before reduction of plates.

processes extending forward from base of anterodorsal lobe (Fig. 138C), one small lobe below insertion of tubular processes void of spinulae (Fig. 138B), entire aedeagal stalk and small band between conical lobes bearing small stout spinulae (Fig. 138A).

Female. — Macropterous. Length of forewings 10-11 mm. General body color, and head-pronotal pigment patterns similar to male. Subgenital plate variable, usually broad-angulate with simple or notched median nipple, produced posteriorly approximately 1/4 to 1/2 length of 9th sternum (Figs. 139 & 141); sometimes without nipple (Fig. 144).

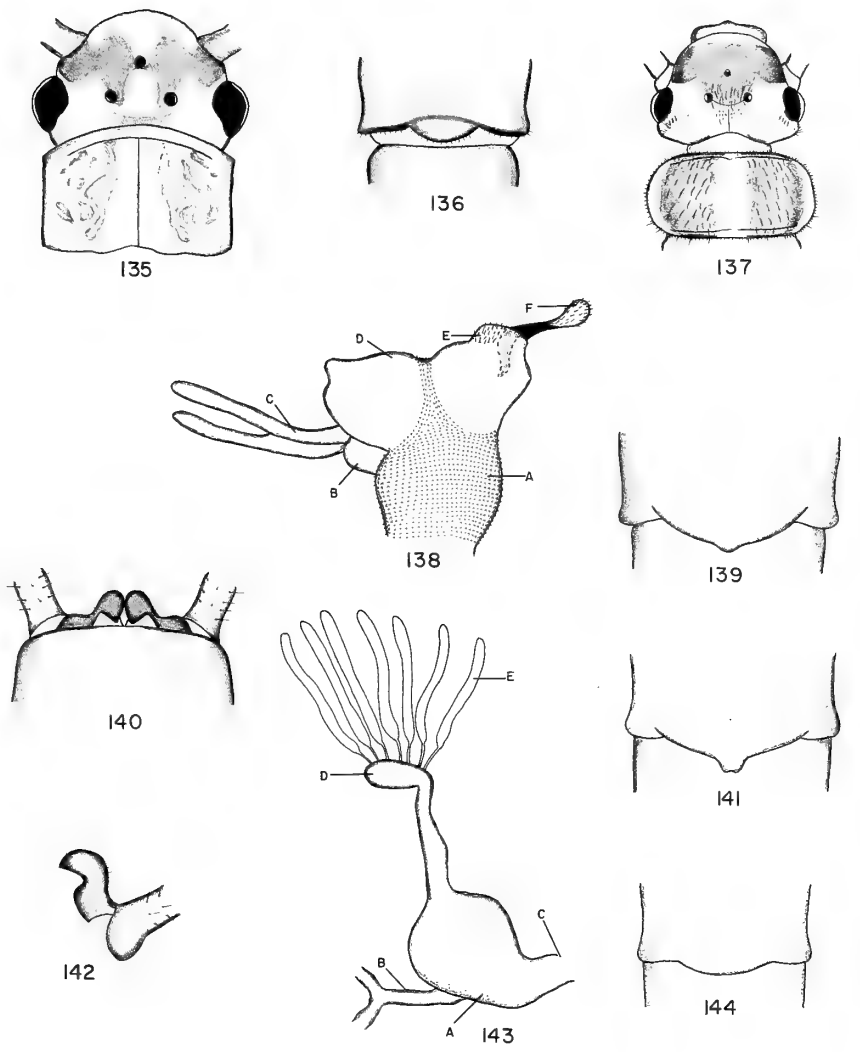
Vagina with narrow ventral band of small stout spinulae (Fig. 143A), seminal receptacle (Fig. 143D) with 6-7 accessory receptacular glands (Fig. 143E).

Nymph (Reared). — Length of mature male nymph 11-12 mm; mature female nymph 13-15 mm. Dorsum of head with large "U"-shaped light yellow area between compound eyes; interocellar space and entire frons anterior to middle antennal bases dark (sometimes with light spot forward of median ocellus); dark band from each eye to occiput; occipital ridge with scattered small, fine spinulae (Fig. 137). Pronotum with median yellow stripe and lateral margins; rest dark brown; margin fringed with evenly spaced, small, stout setae, occasional long setae interspersed at upper and lower angles and posterior margin (Fig. 137). Femora with light dorsal fringe of long hairs and outer surface covered with spine-like setae; tibiae with heavy dorsal fringe of long hairs; ventral margin with row of medium-length hairs and ventral row of short, stout setae. Abdominal terga with 3 longitudinal stripes, 2 wide, dark brown lateral stripes and one narrow median light brown stripe. Posterior margin of cercal segments with whorl of small stout setae.

Ova. — General shape oval, anterior 1/2 always dented, cross section posterior 1/2 round (Fig. 129). Color medium brown. Length .26 mm; width .19 mm. Collar developed, depressed at base, with outer partitions (Figs. 129 & 130).

Material examined. — TYPES: *I. fulva,* Holotype ♂, and allotype ♀, *USA* — UTAH: Case Co., Logan R., 17/VI/1926, J. G. Needham (CU #1,687). Paratypes, 1 ♂, 4 ♀, UTAH: Cache Co., Logan R., 15/VI/1926, J. G. Needham (CU #1,687). *Isoperla chrysannula,* Holotype ♂, and allotype ♀, *USA* — WASHINGTON: Tokul Crk., 16/V/1931, G. N. Hoppe (TBM). Paratypes, WASHINGTON: King Co., Snoqualmie, Snoqualmie Falls, 24/IV/1931, G. N. Hoppe, 1 ♂, Snoqualmie, 2/IV/1932, G. N. Hoppe, 1 ♂, 2 ♀ (TBM), Bothel, 13/IV/1931, G. N. Hoppe, 1 ♂ (TBM), Nisqually R., 30/IV/1931, G. N. Hoppe, 1 ♀ (TBM), Renton, 31/V/1913, Collector ?, 2 ♂, 1 ♀ (TBM). *I. chrysannula,* Holotype ♂, *USA* — WASHINGTON: Mason Co., Shelton, 29/IV/1931, G. N. Hoppe (TBM). Additional specimens — *CANADA* — ALBERTA, Waterton Lake, Kootenai R., 1/VIII/1970, A. R. Gaufin, 1 ♀ (UU), Waterton Lake, 23/VII/1923, J. McDonnough, 1 ♂, 1 ♀ (CU); BRITISH COLUMBIA, Vedder Crossing, Chilliwack R., 26/IV/1937, W. E. Ricker, 20 ♂, 6 ♀, 60 nymphs (INHS), Cultus Lake, 1937, W. E. Ricker, 1 ♂, 1 ♀ (INHS), Vedder Crossing, 9/V/1937, W. E. Ricker, 4 ♂, 2 ♀ (WR), Lakelse R., 15/VI/1950, F. Neave, 1 ♀ (WR), near Falls Wells Gray Park, Clearwater R., 11/VII/1957, W. E. Ricker, 2 ♂, 3 ♀ (WR), Vedder Crossing, 14/VI/1957, W. E. Ricker, 4 ♂, 5 ♀ (WR), Cultus Lake, Hatchery Crk., 31/III/1937, W. E. Ricker, 1 nymph (WR), Big Qualieum, 3 mi. below Horne Lake,

FIGURES 135-144. — *I. fulva.* 135. adult head and pronotum (scale: 1 mm = .06 mm). 136. male vesicle and 8th sternum (1 mm = .05 mm). 137. nymph head



and pronotum (1 mm = .10 mm). 138. male aedeagus, lateral aspect, A. band of small stout spinulae, B. small mesoanterior lobe void of spinulae, C. tubular processes, D. large anterodorsal conical lobe, E. patch of long stout spinulae, F. sclerotized process (1 mm = .03 mm). 139. female subgenital plate, typical (1 mm = .06 mm). 140. male terminalia, dorsal aspect (1 mm = .04 mm). 141. female subgenital plate, variation (1 mm = .06 mm). 142. male paraproct, lateral aspect (1 mm = .02 mm). 143. female vagina, A. vaginal armature, B. oviduct, C. subgenital plate, D. seminal receptacle, E. accessory receptacular glands (1 mm = .03 mm). 144. female subgenital plate, atypical variation (1 mm = .06 mm).

24/V/1953, W. E. Ricker, 9 ♀, 3 exuviae (WR). *USA* — CALIFORNIA: Plumas Co., N. Fork Feather R., Elv. 2,300 feet, 11/XI/1954, P. Chandler, 1 ♀ (SJ). COLORADO: Archuleta Co., Hwy. 84, Toponas Crk., 26/VI/1962, Collector ?, 3 ♀ (UU); Unknown Crk. 2 mi. W. of Big Rock Crk. Hwy. 84, 26/VI/1962, Collector ?, 1 ♀ (UU), Hwy. 84, Big Rock Crk., 26/VI/1962, A. R. Gaufin, 5 ♂ (UU); Beaverhead Co., Dillon, Hwy. 6, Blue R., 30/VII/1960, Collector ?, 1 ♀ (UU); Chaffee Co., Hwy. 24, Granite, Arkansas R., 12/VII/1961, Collector ?, 3 ♂, 5 ♀ (UU), 10 mi. W. of Buena Vista, Cottonwood Lake, 30/VI/1974, S. J. Herman, 2 ♂, 2 ♀ (RWB); Conejos Co., Hwy. 17, 3 mi. E. of Lamanga Pass, Conejos R., 7/V/1976, S. W. Szczytko and K. W. Stewart, 4 nymphs (SWS & NTSU); Eagle Co., Hwy. 24 near Tennessee, Eagle R., 29/VI/1962, Collector ?, 37 ♂, 12 ♀ (UU), Hwy. 24, 2 mi. S. of Camp Hale, Eagle R., 12/VII/1961, Collector ?, 7 ♂, 3 ♀ (UU), East Lake Crk., near Edwards, 29/VI/1962, Collector ?, 6 ♂ (UU), Hwy. 24, 2 mi. S. of Camp Hale, Eagle R., 12/VII/1961, Collector ?, 5 ♂ (UU), Hwy. 24 near Tennessee, Eagle R., 29/VI/1962, Collector ?, 3 ♀ (UU); Grand Co., W. of Granby, Colorado R., 20/VI/1961, Collector ?, 4 ♀ (UU), Rocky Mt. National Park, Mill Crk., 27/VII/1960, A. R. Gaufin, 1 ♂ (UU), Hwy. 40 W. of Granby, Colorado R., 27/VI/1962, Collector ?, 10 ♂, 4 ♀ (UU), Rocky Mt. National Park, Fall R., 24/VII/1960, Collector ?, 1 ♀ (UU), W. of Granby, 20/VI/1961, A. R. Gaufin, 1 nymph (UU); Gunnison Co., 4 mi. above junct. with Gunnison R., Talor R., 12/VII/1962, Collector ?, 2 ♂ (UU), Lake Fork of Gunnison R., 5 mi. below Hwy. 149 at Roadside Park, 27/VI/1964, A. R. Gaufin, 2 ♂ (UU), Cebolla Crk., at junct. with Spring Crk., 13/VII/1962, Collector ?, 6 ♂, 2 ♀ (UU), W. Elk Crk. at Hwy. 50, 15/VI/1962, Collector ?, 4 nymphs (UU), W. Elk Crk., above Gunnison R., 20/VI/1962, A. R. Gaufin, 5 nymphs (UU), Soap Crk., 14/VI/1962, A. R. Gaufin, 4 nymphs (UU), Slate R. below Crested Butte, 12/VII/1962, A. R. Gaufin, 1 nymph (UU), Cebolla Crk., at junct. with Spring Crk., 13/VII/1962, A. R. Gaufin, 1 nymph (UU), 1/4 mi. above Hwy. 50 elevation 7,400 feet, E. Elk Crk., 20/IV/1962, Collector ?, 25 nymphs (UU); Hinsdale Co., 1/2 mi. above Lake San Cristobal, Lake Fort of the Gunnison R., 14/VII/1962, Collector ?, 2 ♂, 1 ♀ (UU), Lake Fort of the Gunnison R., 17/VI/1962, A. R. Gaufin, 61 nymphs (UU); La Plota Co., Lightner Crk. in Canyon, 4/IV/1961, A. R. Gaufin, 3 nymphs (UU); Larimer Co., Rocky Mt. National Park, Hidden Valley Crk., 24/VII/1960, Collector ?, 1 ♀ (UU); Mesa Co., Grand Mesa, stream at canyon 9,000 feet, 27/VI/1961, S. G. Jewett, 4 ♂, 4 ♀ (SJ); Mineral Co., Wolf Crk. Pass, 21/VII/1938, D. J. and J. N. Knull, 291 ♂ (OS[2]); Montrose Co., Hwy. 50, Camarron Crk., 20/IV/1962, A. R. Gaufin, 1 nymph (UU); Park Co., 3 mi. N. of Como, Tarryall Crk., 8/VIII/1973, R. W. Baumann and B. P. Stark, 3 ♂, 2 ♀ (BS); Routt Co., Oak Crk., 22/VI/1968, B. R. Oblad, 4 ♂, 2 ♀ (UU), Beat R., 16/VII/1968, B. A. Oblad, 2 ♂, 5 ♀ (UU), Yampa, Yampa R., 19/VI/1961, A. R. Gaufin, 4 ♂, 3 ♀ (UU), Yampa, Yampa R., 22/VI/1968, B. R. Oblad, 6 ♀ (UU), Morrison Crk., 24/VI/1968, B. R. Oblad 1 ♀ (UU), Willow Cabins bridge, Yampa R., 22/VI/1968, B. R. Oblad, 2 ♂, 2 ♀ (UU), Green Crk., 16/VI/1968, B. R. Oblad, 1 ♀ (UU), Clark, Elk R., 17/VII/1968, B. R. Oblad, 1 ♂, 1 ♀ (UU), Big Crk., 18/III/1968, B. R. Oblad, 3 nymphs (UU), Steamboat Springs, Butcher Knife Crk., 18/III/1968, B. R. Oblad, 9 nymphs (UU), Hunt Crk., 18/III/1968, B. R. Oblad, 8 nymphs (UU), Trout Crk., 11/V/1968, B. R. Oblad, 1 nymph (UU), Yampa, Yampa R., 2/VI/1968, B. R. Oblad, 3 nymphs (UU), Hwy. 131 E. of Yampa, Yampa R., 26/VI/1962, Collector

?, 8 ♂, 1 ♀ (UU); Yampa Co., Yampa R., 19/VI/1961, Collector ?, 1 ♂ (UU); County ?, Webster, Aug., Oslar, 1 ♂ (CU). IDAHO: Bearlake Co., 1 mi. N. of Geneva Hwy. 89 elevation 6,350 feet, Salt Crk., 29/VI/1964, J. W. Richards and S. L. Jensen, 4 ♂, 3 ♀ (UU), Montrelier Crk., junct. Hwy. 89 elevation 6,200 feet, 29/VI/1964, J. W. Richardson and S. L. Jensen, 3 ♂, 4 ♀ (UU), Thomas Fork Crk. at junct. Hwy. 89, 1/2 mi. N. of Geneva, 29/VI/1964, J. W. Richardson and S. L. Jensen, 1 ♀ (UU), Bonneville Co., Pine Crk. at junct. Hwy. 31, 7 mi. N. Swan Valley elevation 5,900 feet, 21/VI/1964, J. W. Richardson and S. L. Jensen, 1 ♂ (UU); Boise Co., N. fork of Poytlo R. at Horseshoe bend, 17/VI/1964, Collector ?, 1 ♂ (UU), S. fork of Poyetlo R. at junct. with N. fork, 17/VI/1964, Collector ?, 2 ♂, 3 ♀, 1 exuvia (UU); Franklin Co., 1 mi. W. Mapleton at Sugar Crk. Bridge, Cub R., 20/VI/1964, J. W. Richardson and S. L. Jensen, 1 ♂, 2 nymphs (UU); Fremont Co., Head Worm R., 19/VI/1955, S. G. Jewett, 1 ♂ (UU); Idaho Co., Warm R., 17/V/1952, S. G. Jewett, 4 ♂, 2 ♀ (SJ), Lochsa R. at junct. with Selway R., 19/VI/1964, 2 ♂, 1 exuvia (UU), 8 mi. above Hwy. 13 on Hwy. H, S. fork of Clearwater R., 18/VI/1964, Collector ?, 1 ♀ (UU), junct. of stream with S. fork of the Clearwater R. 13 mi. below Elk City, 18/VI/1964, Collector ?, 1 nymph (UU); Lemhi Co., Salmon elevation 2,949 feet, 9/VI/1928, C. Wakeland, 3 ♂, 2♀ (CU), Hwy. 93 near Ellis, Salmon R., 19/VI/1964, Collector ?, 1 ♀ (UU), Hwy. 93, N. of Salmon, Bogle Crk., 17/VI/1965, A. R. Gaufin, 14 ♂, 10 ♀ (UU), N. fork of Salmon R., Hwy. 93, 18/VI/1964, Collector ?, 1 ♂, 1 ♀ (UU), Bogle Crk., Hwy. 93, N. of Salmon, 19/VI/1964, Collector ?, 9 ♂, 2 ♀ (RWB), N. fork of Salmon R., 17/VI/1965, A. R. Gaufin, 9 ♂, 7 ♀ (RWB), N. of Challis, Salmon R., 19/VI/1963, Collector ?, 1 ♂ (UU), 1 mi. N. of N. fork of Salmon R., 17/VI/1965, A. R. Gaufin, 7 ♂, 3 ♀ (UU). MONTANA: Beaverhead Co., Dillon, Big Hole R., Hwy. 19 N., 16/VI/1967, A. R. Gaufin, 18 ♂, 7 ♀ (UU), 15 mi. S. of Dillon, Beaverhead R., 19/V/1965, A. V. Nebeker, 17 ♂, 10 ♀ (RWB), N. of Dillon, Beaverhead R., 16/VI/1967, A. R. Gaufin, 7 ♂, 18 ♀ (UU), Red Rock R., 28/VI/1973, G. F. and C. H. Edmunds, 5 ♂ (BS); Broadwater Co., 15 mi. E. of Townsend, Deep Crk., 8/VII/1966, J. R. Grierson, 1 ♀ (UU), Missouri R. Bridge at Toston, 11/V/1950, Collector ?, 5 ♂, 5 ♀ (UU), Toston, Missouri R. Bridge, 8/V/1949, R. Hays, 5 ♂, 2 ♀, 3 nymphs (UU); Carson Co., E. Rosebud Crk., 21/VI/1966, J. R. Grierson, 4 ♂, 1 ♀ (UU); Cascade Co., Belt Crk., 7/VII/1966, Collector ?, 2 ♂ (UU); Fergus Co., Big Spring Crk., 16/IV/1952, N. A. Thoreson, 10 ♂, 5 ♀ (UU); Flathead Co., N. fork of Flathead R., 7/VII/1973, J. Stanford, 3 ♂, 2 ♀ (JS), Bowman Crk., 24/VII/1970, A. R. Gaufin, 2 ♀ (UU), N. fork of Flathead R. at Stat. 5, 7/VII/1973, J. A. Stanford, 3 ♂, 2 ♀ (JS); Gallatin Co., 3 mi. W. 3 Forks, Jefferson R., 2/V/1972, Roemhild, 2 ♂, 1 ♀ (TSU); W. Gallatin R., 6/VII/1951, R. Hays and J. Bailey, 1 ♀ (UU), W. Gallatin R., 13/VI/1951, Collector ?, 24 ♂, 15 ♀ (UU), Bozeman, Hoffman Crk., 20/VI/1950, R. Hays, 4 ♂, 1 ♀ (UU), Hwy. 191 near Baconrind, W. Gallatin R., 26/VII/1963, A. R. Gaufin, 12 ♂, 8 ♀ (UU), Hyalite Crk., 3/VIII/1950, Collector ?, 2 ♀ (UU), Madison R. above Hebgen Lake, 24/VI/1964, J. W. Richardson and S. L. Jenson, 4 nymphs (UU); Glacier Co., Glacier National Park, St. Mary's R. at St. Mary's Campground, 30/VII/1965, A. R. Gaufin, 2 ♀ (UU), Hwy. 89 E. of Glacier Park, Cutbank Crk., 22/VII/1966, A. R. Gaufin, 1 ♀ (UU), Cutbank Crk., 18/VII/1965, A. R. Gaufin, 1 ♀ (UU), Hwy. 89 near Babb, St. Mary's R., 23/VII/1966, A. R. Gaufin, 2 ♂, 5 ♀ (UU), St. Mary's Campground, St. Mary's R., 10/VII/1964, A. R. Gaufin, 4 ♂, 1 ♀ (UU), entrance to

Glacier National Park, Sherrburne Crk., 7/VII/1966, A. R. Gaufin, 3 ♂, 6 ♀ (UU), St. Mary's Campground, St. Mary's R., 23/VII/1966, A. R. Gaufin, 16 ♂, 28 ♀ (UU); Granite Co., Hwy. 10A near Phillipsburg, Flint Crk., 16/VI/1967, A. R. Gaufin, 18 ♂, 8 ♀ (UU), Flint Crk., Hwy. 10A near Phillipsburg, 16/VI/1967, A. R. Gaufin, 18 ♂, 6 ♀ (UU), Stoney Crk., 28/VI/1967, M. L. Miner, 15 ♂, 7 ♀ (RWB), Rock Crk., 28/VI/1967, R. L. Newell, 26 ♂, 17 ♀ (UU), Hwy. 10A near Phillipsburg, Flint Crk., 16/VI/1967, A. R. Gaufin, 20 ♂, 10 ♀ (UU), Rock Crk., 4/IV/1969, B. R. Oblad, 11 nymphs (UU); Judith Basin Co., Judith R., 2/VIII/1967, J. R. Grierson, 1 ♂, 1 ♀ (UU), Arrow Crk., 7/VII/1966, J. R. Grierson, 1 ♀ (UU); Lake Co., Hwy. 209, Leon Crk., 24/VI/1964, A. R. Gaufin, 5 ♂, 3 ♀ (UU); Lewis and Clark Co., Hwy. 20 E. of Bonner, Blackfoot R., 23/VII/1967, A. R. Gaufin, 28 ♂, 26 ♀ (UU), Keepcool Crk., 1/VII/1969, R. L. Newell, 5 ♂, 2 ♀ (UU); Meagher Co., 15 mi. above Smith R., Thomas Crk., 8/VII/1966, J. R. Grierson, 1 ♂, 1 ♀ (UU), Sheep Crk., 7/VII/1966, J. R. Grierson, 1 ♂ (UU), 2 mi. N. of White Sulphur Springs, Smith R., 8/VII/1966, J. R. Grierson, 2 ♂, 1 ♀ (UU), Clearwater R., Alva Lake outlet, 1/VII/1969, R. L. Newell, 2 ♀ (UU), Spring Crk., 1/VII/1966, J. R. Grierson, 1 ♂, 1 ♀ (UU); Missoula Co., Warm Spring Camp, Bitterroot R., 19/VII/1963, Collector ?, 1 ♂, 1 ♀ (UU), Blackfoot R., 8/VII/1969, R. L. Newell, 1 ♂, 6 ♀ (UU), 16.4 mi. above Hwy. 93, Lolo Crk., 16/VII/1965, J. R. Grierson, 2 ♀ (UU), 17 mi. above Bitterroot R., Miller Crk., 20/VII/1965, J. R. Grierson, 1 ♀ (UU), 5 mi. W. of Lolo, Lolo Crk., 29/VI/1964, A. R. Gaufin, 35 ♂, 24 ♀ (UU); Park Co., Shields R., 1/VII/1966, J. R. Grierson, 6 ♂, 4 ♀ (UU); Powell Co., Monture Crk., 1/VII/1969, R. C. Newell, 4 ♂ (UU), Hwy. 200, Monture Crk., 11/VI/1970, A. R. Gaufin, 2 ♀ (UU); Ravalli Co., Woodside, Bitterroot R., 18/V/1955, D. R. Mariekey, 6 ♂, 2 ♀ (UU), above E. fork, Bitterroot R., Camp Crk., 22/VI/1965, J. R. Grierson, 1 ♀ (UU), E. fork of Bitterroot R., 10 mi. above junct. with W. fork, 28/VI/1965, J. R. Grierson, 1 ♂, 2 ♀ (UU), 1 mi. above Hwy. 93, Warm Springs Crk., 24/VII/1965, J. R. Grierson, 1 ♀ (UU), E. fork of Bitterroot R., 10 mi. above junct. with W. fork of Bitterroot R., 22/VI/1965, J. G. Grierson, 2 ♂, 3 ♀ (UU), Hwy. 93, Warm Springs Camp, Bitterroot R., 29/VII/1963, Collector ?, 3 ♂, 1 ♀ (UU), E. fork of Bitterroot R. at Sula Post Office Hwy. 93, 27/VI/1964, A. R. Gaufin, 1 ♂, 1 ♀ (UU), S. fork of Bitterroot R. at Sula Ranger Station, 27/VI/1964, A. R. Gaufin, 3 ♂, 6 ♀ (UU); Sanders Co., Hwy. 93, N. of Jocko Camp, 2 mi. S. of Ravalli, Jocko R., 20/VI/1963, A. R. Gaufin, 14 ♂, 9 ♀ (UU); Stillwater Co., Stillwater R., 25/VI/196-, J. R. Grierson, 5 ♂, 2 ♀ (UU); Sweet Grass Co., 21 mi. S.W. of Big Timber, Boulder R., 28/VI/1966, J. R. Grierson, 15 ♂, 6 ♀ (RWB), Sweet Grass Canyon above Hwy. 29, 30/VI/1966, J. R. Grierson, 1 ♂, 2 ♀ (UU); Bridger Crk., 24/VI/1966, J. R. Grierson, 4 ♂, 1 ♀ (UU); Teton Co., Teton R. at junct. Hwy. 33, 2 mi. W. of Tetonia, 22/VI/1964, J. W. Richardson and S. L. Jensen, 1 ♂, 2 ♀ (UU), N. fork of Teton R. at junct. Hwy. 32, 22/IV/1964, J. W. Richardson and S. L. Jensen, 1 nymph (UU); County ?, W. fork of Madison R., 8/VIII/1972, Collector ?, 2 ♀ (ISU), County ?, Babb, Swift Crk., 13/VII/1963, Collector ?, 2 ♂, 3 ♀ (UU), Potomac, Big Blackfoot R., 20/VI/1966, F. E. Barry, 1 ♂, 1 ♀ (CU). NEVADA: Eklo Co., Hwy. 11, Secret Crk., 15/VI/1974, B. P. Stark, 15 ♀ (BS), Secret Crk. at Secret Pass, 15/VI/1974, B. P. Stark, 9 ♂, 5 ♀ (BS). NEW MEXICO: Colfax Co., Cimarron Canyon, Ute Park, 12/VI/1956, Collector ?, 1♂ (WR); San Miguel Co., near Terrero, Holy Ghost Crk., 19/VI/1961, S. G. Jewett, 4 ♂ (SGJ); Taos Co., Pan-

chuela near Cowler, 9/VII/1944, W. J. Coster, 1 ♂ (WR). OREGON: Clackamas Co., Big Eddy, 1/VI/1952, S. G. Jewett, 7 ♂, 5 ♀ (LCMNH), Hwy. 26 at Brighton, Salmon R., 24/VI/1967, R. W. Baumann, 1 ♂, 5 ♀ (RWB); Clatsop Co., Big Crk., 16/IV/1949, S. G. Jewett, 2 ♂ (LCMNH), Young R., 13/IV/1947, S. G. Jewett, 2 nymphs (SJ), Big Crk., 16/IV/1949, S. G. Jewett, 5 nymphs (SJ), Grant Co., middle fork of John Day, 29 mi. S. of Ukian, Hwy. 395, 29/IV/1977, Dunster, 1 ♂, 1 ♀, 1 nymph (CWS); Jackson Co., 4 mi. W. Dead Indian, Soda Spring, 21/V/1964, J. Schuh, 1 ♂, 1 ♀ (CU); Lake Co., Chewaucan R. dam site, 18/VI/1955, J. Schuh, 1 ♀ (OS[2]), Chewaucan R., 18/VI/1955, J. Schuh, 1 ♀ (OS[2]); Modoc Co., Pit R., 28/IV/1977, Dunster, 2 ♀ (CWS); Wallowa Co., Minam, Wallowa Canyon Fount., 21/VII/1929, H. A. Scullen, 1 ♂ (CU); County ?, Burnt R., near Lime, 20/IV/1954, W. Ricker, 5 ♂, 1 ♀, 5 exuviae (WR), Rock Crk., E. of Miteil, 6/V/1970, S. G. Jewett, 2 ♂, 1 ♀ (SJ). UTAH: Boxelder Co., 5 mi. E. Brigham City, Boxelder Crk., 29/VI/1952, C. J. D. Brown, 1 ♀, 1 nymph (UU); Cache Co., Logan, 23/VI/1907, E. G. Titus, 1 ♀ (CU), Logan Canyon, 27/VI/1937, W. P. Nye, 1 ♂, 1 ♀ (SWS & NTSU), Logan Canyon, Logan R., 18/VI/1960, G. F. Knowlton, 6 ♂, 3 ♀ (UU), Logan Canyon, 7/VII/1939, D. J. and J. N. Knull, 7 ♀ (OS[2]), Logan R., 12/VII/1922, Collector ?, 1 ♂ (CU), Logan R., 26/VI/1926, Collector ?, 1 ♂ (CU), Logan R., 18/VI/1926, Collector ?, 1 ♂ (CU), Logan R., 16/VI/1926, Collector ?, 1 ♂, 1 ♀ (CU), Logan, 4/VI/1903, Collector ?, 1 ♂ (CU), Logan Canyon, 7/IV/1966, W. P. Nye, 2 ♂, 4 ♀ (UU); Duchesne Co., Unita R. at Wandin Campground, 7/VIII/1975, R. W. Baumann, 2 ♂, 3 ♀ (RWB), Uinta Campground, Uinta R., 7/VIII/1975, R. W. Baumann, 2 ♂ (RWB); Emery Co., Ferron Picnic ground above Hwy. 10, Ferron Crk., 12/V/1976, S. W. Szczytko and K. W. Stewart, 6 nymphs (SWS & NTSU); Grand Co., Manti-La Sal National Forest, Hunting Canyon 2 1/2 mi. E. of Boulyar Camp, 3/VII/1949, L. G. Gunderson, 3/VII/1949, 1 ♀ (UU); Lake Co., Swan R., 8/VII/1967, Milan, 24 ♀ (UU); Rich Co., Big Crk. above Randolph, 17/VI/1975, R. W. Baumann, 3 ♂ (RWB); Salt Lake Co., Mill Crk., Porter Fork, 1-/VI/1972, B. P. Stark, 1 ♀ (BS), Mill Crk., 1000 Springs, 16/VI/1972, B. P. Stark, 1 ♀ (BS), Big Cottonwood Crk., 14/VII/1966, R. W. Baumann, 1 ♂, 2 ♀ (UU), Emigration Canyon Crk., 12/VI/1966, R. W. Baumann, 25 nymphs (RWB), Church Fork, Mill Crk., 16/VI/1972, B. P. Stark, 1 ♂, 1 ♀ (BS), Little Dell Crk., 17/VI/1965, R. W. Baumann, 1 ♂ (UU), Big Cottonwood Crk. at Silver Fork, 14/VII/1966, R. W. Baumann, 1 ♀ (UU), Mill Crk., Canyon Crk., 9/VI/1966, R. W. Baumann, 4 ♂, 2 ♀ (RWB), American Forks Canyon, Date ?, Hubard and Schwarz, 1 ♂ (CU), Parley's Crk. above Mt. Dell, 5/VI/1963, A. V. Nebeker, 2 nymphs (UU), Emigration Canyon Crk., 2/V/1966, R. W. Baumann, 1 nymph (UU), Mill Crk. Canyon Crk., 15/V/1965, R. W. Baumann, 5 nymphs (UU), Mill Crk., Canyon Crk., 11/IV/1966, R. W. Baumann, 1 ♂, 8 ♀, 3 nymphs (SGJ), Little Dell Crk., 26/V/1965, R. W. Baumann, 9 nymphs (RWB), Cardiff Fork Bridge, Big Cottonwood Crk., 29/VI/1966, R. W. Baumann, 7 ♂, 1 ♀ (RWB), City Crk. near spring, 1/4 mi. above caretakers, 29/III/1966, Uresh, 6 nymphs (UU); Summit Co., Silver Crk., 9/VI/1961, R. W. Baumann, 1 ♂, 2 ♀ (UU), Weber R., Middle Fork, 5/VIII/1975, Sakamoto et al., 2 ♀ (RWB), Weber R. near Oakley, 5/VII/1975, Sakamoto et al., 1 ♂ (RWB), W. F. Blocks Fork R., 4/VII/1975, R. W. Baumann, 1 ♂ (RWB), Provo R. at Vivian Park, 2/VII/1954, A. R. Gaufin, 14 ♂, 10 ♀ (UU), Weber R. below Ploa, 17/V/1967, B. R. Oblad, 5 nymphs (UU), Brigham Canyon, 14/V/1937, Knowlton and Harmston, 1 ♂, 2 ♀ (INHS),

Weber R. at Piney Resort, 23/I/1960, S. C. Jorgenson, 20 nymphs (UU), E. Canyon Crk. bridge, 2 mi. above reservoir, 7/VII/1965, R. W. Baumann, 1 ♂, 12 ♀ (RWB); Utah Co., Provo R., 24/VII/1971, J. W. Aaron, 3 ♂, 1 ♀ (BYU), Dry Canyon Crk. at Hwy. 80, 7/IV/1966, R. W. Baumann, 7 nymphs (UU), American Fork Canyon, 15/IV/1967, B. R. Oblad, 16 nymphs (RWB); Weber Co., Ogden R. below Pine R. dam, 2/V/1968, R. W. Baumann, 8 ♂, 7 ♀ (RWB), Pine Valley, 28/VI/1937, D. J. and J. N. Knull, 1 ♀ (OS[2]), E. Canyon Crk. at Kimball junct. 15 E. of Provo, 13/V/1976, S. W. Szczytko and K. W. Stewart, 26 nymphs (SWS & NTSU). WASHINGTON: Rajumy R., 20/IV/1932, Collector ?, 1 ♀ (UW), Snoqualmie, 16/V/1931, Collector ?, 1 p (UW); Kittitas Co., Cle Ella, 15/VII/1932, D. R. Hoppe, 1 ♀ (UW), Ellensburg, Jakima R., 8/VIII/1882, S. Hendshaw, 1 ♂ (UW); Shamama Co., Mt. Adams Area, Lewis R., 31/VIII/1958, Collector ?, 1 nymph (UW); Thurston Co., Olympia, 2/VI/1895, Collector ?, 1 ♀ (CU); County ?, Nesquelly R., 2/V/1931, Collector ?, 1 ♀ (UW). WYOMING: Carbon Co., Medicine Bow Mts., Top of Pass, 14/VIII/1947, Ross and Ross, 1 ♂ (WR), Riverside, Madison R., 2/V/1964, Collector ?, 3 nymphs (UU); Lincoln Co., at junct., Hwy. 26 2 mi. N. of Smoot, Salt R., 29/VI/1964, J. W. Richardson and S. L. Jensen, 4 ♂, 3 ♀ (UU); Park Co., S.E. of Cooks City, Clarks Fork of Yellowstone R., 28/VII/1966, J. R. Grierson, 1 ♂, 2 ♀ (UU), Cascade Camp, Yellowstone R., 6/VII/1951, A. R. Gaufin, 1 ♂ (UU); Sublette Co., N. of Cora, Willow Crk., 18/VII/1962, Collector ?, 1 ♂ (UU), Daniel, Green R., 19/VII/1972, B. P. Stark, 1 ♂ (BS), 21 mi. N. of Cora, Green R., 19/VII/1972, B. P. Stark, 2 ♂ (BS), Spider Web, Pine Crk. at Pinedale, 20/VII/1972, B. P. Stark, 1 ♂ (BS); Teton Co., junct. Hwy. 26 and 89, Hoback R., 23/VI/1964, S. L. Jensen and J. W. Richardson, 5 nymphs (UU), 7 mi. N. of Jackson, Gros Ventre R., 23/VI/1964, S. L. Jensen and J. W. Richardson, 11 nymphs (UU), 3 mi. S. of canyon junct., Yellowstone R., 26/VI/1964, S. L. Jensen and J. W. Richardson, 8 nymphs (UU), Grand Teton National Park, Snake R., 28/VI/1964, S. L. Jensen and J. W. Richardson, 2 nymphs (UU), Yellowstone National Park, 1921, J. T. Needham, 2 ♀, 1 nymph (CU), near Jackson, Hoback R., 6/VII/1936, H. H. Ross, 1 ♂, 5 ♀ (INHS), junct. Hwy. 26 and 187, 7 mi. N. of Jackson, Gros Ventre R., 23/VI/1964, S. L. Jensen and J. W. Richardson, 18 ♂, 16 ♀ (RWB), near Hoback junct., Snake R., 16/VI/1973, J. Perry, 2 ♂, 1 ♀ (RWB), Hwy. 167, Cliff Crk., 14/VII/1962, Collector ?, 1 ♂ (UU), Yellowstone National Park, Gibbon R., 25/VI/1964, S. L. Jensen and J. W. Richardson, 1 ♂ (UU), 10 mi. W. of Thumb, Yellowstone National Park, Crawfish Crk., 27/VII/1964, J. W. Richardson and S. L. Jensen, 5 ♂, 2 ♀ (UU), Moose, Grand Teton National Park, Snake R., 28/VI/1964, J. W. Richardson and S. L. Jensen, 1 ♂ (UU); County ?, Univ. of Wyoming Sci. Camp, Nash Fork Crk., VI/1960, A. F. Bogge, 2 ♂, 2 ♀, 6 nymphs (SJ). UNKNOWN LOCALITIES: County ?, 2 mi. above Ennis Lake, Madison R., 3/V/1970, Collector ?, 2 ♂, 3 ♀ (UU); Lake Co., Salmon Py. Swan R., 20/VII/1962, Milam, 4 ♀ (UU).

Distribution. — CANADA: Alberta, British Columbia; USA: Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington, and Wyoming (Fig. 118).

Diagnosis and Discussion. — This species is very similar to *I. marmorata* (see diagnosis and discussion under *I. marmorata*). It is the most

common western *Isoperla* in collections, from a wide range of lotic habitats.

Knight and Gaufin (1965) found that reducing dissolved oxygen concentrations to 1.0 cc/1, and water flow to 0.004 feet/sec. at 10° C, killed 8 percent of *I. fulva* nymphs within 24 hours, and 100 percent within 144 hours. Knight and Gaufin (1966) reported that *I. fulva* was eurythermic and distributed between 7,000 to 9,200 feet in the Gunnison River drainage system in Colorado. It occurs in temporary streams, high elevation streams, low elevation streams, stony rivers, constant rivers, and sluggish rivers in the Gunnison River drainage system in Colorado, associated most frequently with *Sweltsa coloradensis* (Banks), *Isoperla patricia* = *I. quinquepunctata* (Banks), *Hesperoperla pacifica* (Banks), and *Claassenia sabulosa* (Banks) (Knight and Gaufin 1967).

Richardson and Gaufin (1971) reported that pre-emergent *I. fulva* nymphs were primarily carnivores. Fuller and Stewart (1977) found that newly recruited *I. fulva* nymphs in Oct. were primarily phytophagus, with filamentous algae comprising 47.5 percent, diatoms 15.5 percent, detritus 28 percent, and animal matter 9 percent of their diets. In Dec. the nymphs shifted toward carnivory, feeding increasingly on Chironomidae larvae and Ephemeroptera nymphs, and in May and Jun., pre-emergent nymphs fed primarily on Chironomidae larvae.

My examination of ova from live gravid females revealed that each punctation in the large chorionic depressions contained a rounded proteinaceous body (Fig. 128). These structures are undoubtedly shrunken by alcohol preservation and the dehydration techniques used in preparing ova for SEM study, and therefore do not appear in most of the photographs. When placed in water these bodies spring out, pushing a gelatinous sticky membrane away from the surface, that when fully expanded completely surrounds the ova and offers adhesion to substrates (Figs. 131-133). The patterns of punctations can be observed in the expanded gelatinous membrane (Figs. 131-133). About 2 and one-half min. in water were required for full development of the envelope.

Stanford (unpublished Ph.D. dissertation) found that *I. fulva* in the upper Flathead River, Montana exhibited a univoltine life cycle, with emergence occurring from late May until early Jul. Nymphs first appeared in the river in late Jul.

Adults from the extensive material examined emerged in early May-Aug., with the largest numbers taken from mid-Jun. to early Jul. It is the most common western *Isoperla,* from the widest range of lotic habitat types.

SPECIES GROUP E

Isoperla sordida complex

This group is composed of *I. acula* Jewett, *I. adunca* Jewett, *I. denningi* Jewett, *I. fusca* Needham and Claassen, *I. petersoni* Needham and Christenson, *I. rainiera* Jewett, *I. sordida* Banks, and a new species, *I. bifurcata.* These species all share the following characteristics: 1. long ventral hair at posterior margin of adult cercal segments; 2. male aedeagus with variable sclerotized process, bifurcate at base; 3. well-developed, variable-shaped male vesicle; 4. variable female subgenital plate, usually with a median emargination; 5. short stout hairs and an occasional long hair on margin of nymphal pronotum; 6. chorionic ridges of ova variable and usually well developed; and 7. chorion covered with small punctations.

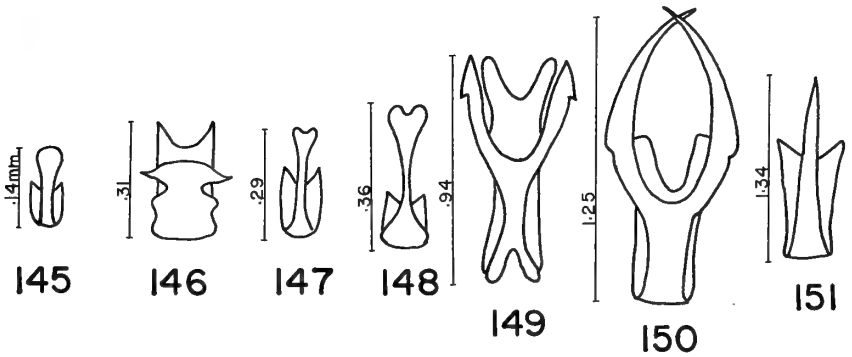
The sclerotized process of the male aedeagus exhibits a distinct phenocline (Figs. 145-151). The base of the process is forked in all species, and the dorsal arm is variously modified from a simple short rod to an elongate forked or unforked process. In *I. adunca* the process is very short, and the simple dorsal arm is narrow and slightly expanded at its apex (Figs. 145 & 160D). In *I. rainiera* the process is short and stout, with a broad dorsal arm bearing 2 lateral downward projecting spines (Figs. 148, 214 & 218D). The dorsal arm of *I. denningi* is elongated, with a slight median emargination at the apex (Figs. 147, 181 & 183C), and in *I. sordida* it has become constricted in the middle and expanded at the base and apex, forming 2 rounded lobes apically bearing short, stout spinulae on the outer margin (Figs. 148, 222, 225E & 226). In *I. bifurcata* the dorsal arm is forked near the base-arm plate and near its midsection, forming 2 moderately long apical arms bluntly pointed at the tips, and each bearing a ventral spine (Figs. 149, 165C & 168). The forked members of the *I. fusca* dorsal arm are curved, very long, and tapered to fine points which cross near the apex; each arm bears a curled ventral spine near the bottom 1/3 of its length (Figs. 150, 189 & 191C). In *I. petersoni* the dorsal arm members have apparently fused into a single long, curved, striolate, needle-like process (Figs. 151 & 207). Placement of *I. petersoni* at this position in the phenocline was also based on the similarity of its ova with *I. fusca.*

This group is concentrated in the western coastal mountain ranges and Northern Rocky Mountains, with one record of *I. petersoni* from Alaska (Fig. 152). Most species inhabit small creeks or springs. Emergence occurs from Apr.-late Oct., and all species probably undergo univoltine life cycles.

Isoperla acula Jewett

Isoperla acula Jewett, 1962, 38:18. Holotype ♂; 7 mi. N.E. of Academy, elevation 800 feet, Fresno, Co., California, USA (CAS) (male genitalia, and head-pronotal pattern).
Isoperla acula, Illies, 1966:393.

Male. — Macropterous. Length of forewings 9-10 mm; length of body 9-10 mm. General body color light brown. Ocelli of head connected by narrow band of dark brown pigmentation; interocellar area and rest of head light (Fig. 153). Pronotum light brown with median yellow stripe, and lateral brown rugosities (Fig. 153). Wings hyaline, veins medium brown. Long ventral hair at posterior margin of each cercal segment. Median of each abdominal tergum with patch of long stout setae, mesoposterior margin of 9th tergum with patch of stout barrel-like spinulae and long fine hairs (156). Paraprocts long, tapering to acute points apically,



FIGURES 145-151. — Phenocline of sclerotized aedeagal structure in the *I. sordida* species complex, 145. *I. adunca,* 146. *I. rainiera,* 147. *I. denningi,* 148. *I. sordida,* 149. *I. bifurcata,* 150. *I. fusca,* 151. *I. petersoni.*

recurving over 1/4 10th tergum (Fig. 155). Vesicle rectangular, row of small fine hairs on apex, darker than rest of segment (Fig. 154). Mesal section of aedeagus bearing patch of concentrated, stout, golden brown spinulae (longitudinal, cylindrical sclerotized structure difficult to observe because of light pigmentation, Jewett, 1962).

Female. — Unknown.

Nymph. — Unknown.

Ova. — Unknown.

Material examined. — Paratypes, CALIFORNIA: Fresno Co., 7 mi. N.E. of Academy, elevation 800 feet, 19/V/1955, D. L. Abell, 2 ♂ (SJ).

Distribution. — USA — CALIFORNIA (Fig. 152).

Diagnosis and Discussion. — *I. acula* is a very rare species, known only from 4 male specimens. Placement in this species group is questionable, and is based entirely on adult pigment patterns of the head and pronotum, and Jewett's (1962) description of the aedeagal sclerotized structure. The terminal portion of the abdomen had been cleared, and

the aedeagus partially everted, in the 2 paratype specimens studied, although the aedeagal sac in both had apparently ruptured and the apical portion was missing, along with the sclerotized process. Discussion of relationships with other species must await association and description of nymphs, females, and ova. Nothing is known of the biology of this rare species.

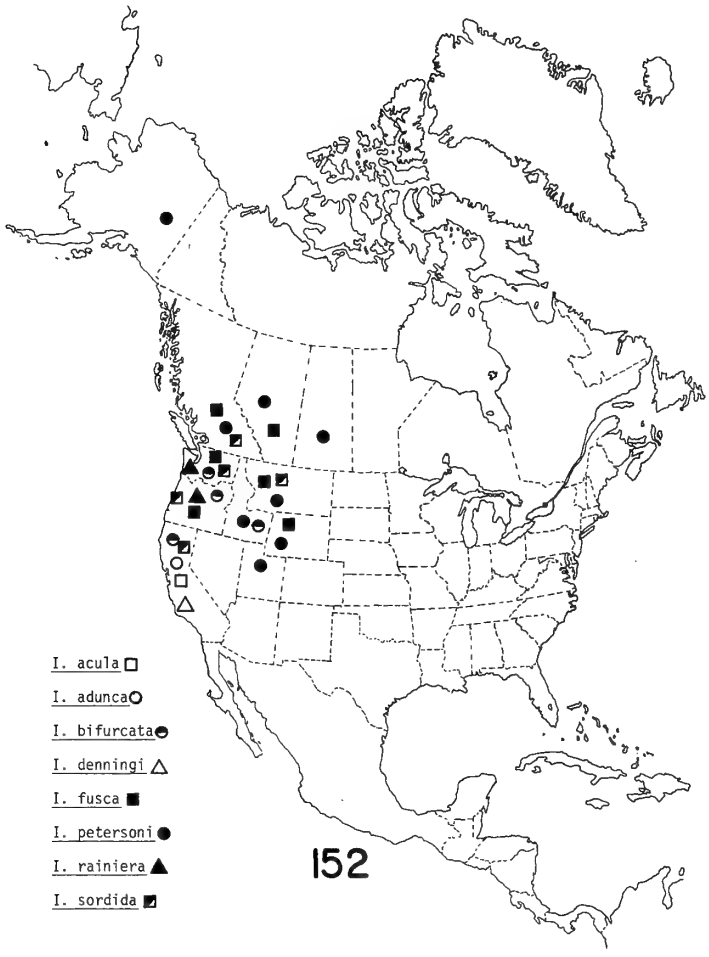
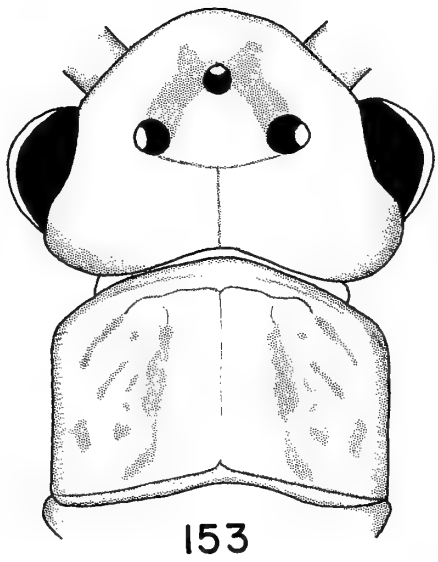


FIGURE 152. — Distribution of the *I. sordida* complex.



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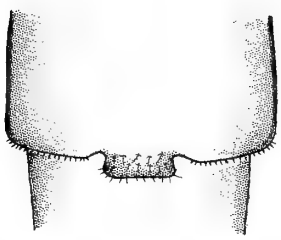

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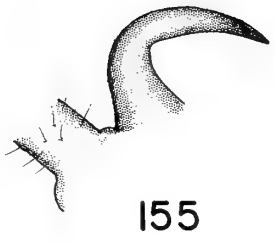

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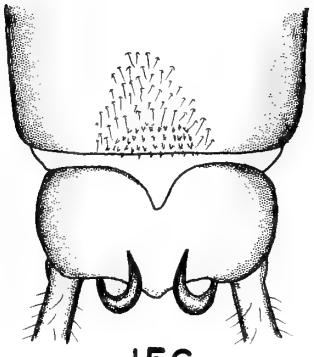

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FIGURES 153-156. — *I. acula.* 153. adult head and pronotum (scale: 1 mm = .03 mm). 154. male vesicle and 8th sternum (1 mm = .03 mm). 155. male paraproct, lateral aspect (1 mm = .01 mm). 156. male terminal, abdominal terga (1 mm = .03).

Isoperla adunca Jewett

Isoperla adunca Jewett, 1962, 38:19. Holotype ♂, and allotype ♀; 5 mi. E. of Mt. Hamilton, Santa Clara Co., California, USA (CAS) (male and female genitalia, and aedeagal structure).
Isoperla adunca, Illies, 1966:393.

Male. — Macropterous. Length of forewings 7-8 mm; length of body 7-9 mm. General body color medium brown. Interocellar area of head dark brown, forming solid, dark equilateral triangle between ocelli (Fig. 157). Pronotum light brown, with median light yellow stripe and small medium-brown rugosities (Fig. 157). Wings distinct, suffused with medium-brown pigment. Antennae and cerci dark brown, posterior margin of cercal segments with one long ventral hair. Paraprocts slender, deflected downward at apex, acute, recurving to level of 10th tergum (Fig. 159). Vesicle narrow at base, lateral margins parallel, apex rounded, with several medium-length hairs (Fig. 158). Aedeagus tubular, with short dorsal sclerotized clavate process, bifurcate at base (Fig. 160D); apex void of spinulae, anterodorsal margin bearing band of concentrated small, fine spinulae (Fig. 160A), posterodorsal margin and mesal section bearing short, stout spinulae and occasional long hair-like spinulae (Fig. 160B); pedicel bearing short, stout spinulae interspersed with long hair-like spinulae (Fig. 160C).

Female. — Macropterous. Length of forewings 9-10 mm; length of body 8-10 mm. General body color and head-pronotal pigment patterns similar to male. Subgenital plate slightly triangulate, rounded posteriorly with median emargination, produced 1/4 to 1/2 length of 9th sternum (Fig. 161).

Nymph. — Unknown.

Ova. — General shape oblong, cross section triangular, except circular at poles (Fig. 173). Color yellowish brown. Length .33 mm; width .23 mm. Collar absent, chorionic ridges thin and elevated, forming lacy, hexagonal cell pattern; small, evenly spaced punctations within cells (Figs. 172-174); cells near bottom 1/3 elongate and triangular (Figs. 172-174). Micropyles small, scattered on ridges of triangular cells on one side (Fig. 175).

Material examined. — TYPES: Holotype ♂, allotype ♀, CALIFORNIA, Santa Clara Co., 5 mi. E. of Mt. Hamilton, 31/V/1949, Collector ?, 1 ♂, 4 ♀ (CAS), 2 ♂, 1 ♀ (SJ). Additional specimens — *USA* — CALIFORNIA: Alameda Co., 17 1/2 mi. S. of Livermore, Arroyo Macho, 27/VI/1965, P. H. Arnaud, Jr., 3 ♂, 6 ♀ (CAS).

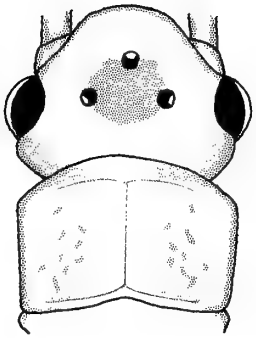
Distribution. — USA — California (Fig. 152).

Diagnosis and Discussion. — This species is similar to *I. denningi* (see diagnosis and discussion under *I. denningi*), although ova are more similar to *I. rainiera.*

This is a rare species restricted to the Coastal Range of California, and no studies on the life history or general biology have been done. It is found in creeks, and emergence occurs from May through Jun.

Isoperla bifurcata NEW SPECIES

Isoperla sordida, Gaufin et al., 1966, 14:71. In part (male and female genitalia, and sclerotized aedeagal process).



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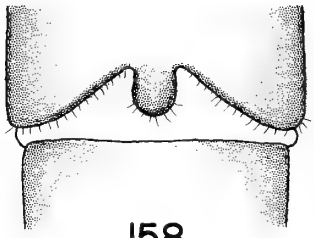

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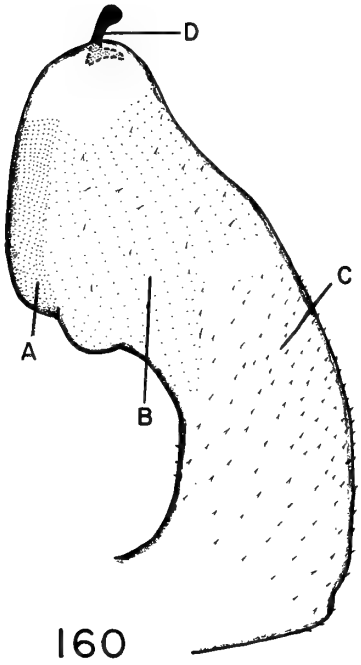

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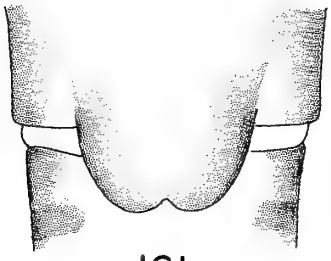

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FIGURES 157-161. — *I. adunca*. 157. adult head and pronotum (scale: 1 mm = .06 mm). 158. male vesicle and 8th sternum (1 mm = .03 mm). 159. male paraproct, lateral aspect (1 mm = .02 mm). 160. male aedeagus, lateral aspect, A. band of concentrated, small, fine spinulae, B. patch of short, stout spinulae and occasional long hair-like spinulae, C. patch of scattered long hair-like spinulae, D. sclerotized process (1 mm = .01 mm). 161. female subgenital plate (1 mm = .03 mm).

Isoperla sordida, Gaufin et al., 1972, 98:119. In part (male and female genitalia, and sclerotized aedeagal process).

Isoperla sordida, Baumann et al., 1977, 31:152. In part (male and female genitalia, and sclerotized aedeagal process).

Male. — Macropterous. Length of forewings 6-9 mm; length of body 8-10 mm. General body color dark brown. Lateral ocelli of head with variable medium-brown band, usually not connected to anterior ocellus; interocellar space light; anterior ocellus with wide, medium-brown band and black, narrow, broadly "U"-shaped anterior band, wide, light brown band extending from front of compound eyes to base of antennae often connected to anterior ocellus; 2 dark brown spots anterior frons (Fig. 162). Pronotum mostly medium-brown, median light stripe, and rugosities dark brown (Fig. 162). Wings fumose, veins dark brown. Abdominal terga with 8 faint rows of longitudinal dots, 2 mesal and 3 each laterally. Posterior margin of cercal segments with long ventral hair. Paraprocts short, stout, tapering slightly toward apex, bearing small, fine hairs, recurving forward to level of 10th tergum (Figs. 166 & 167). Vesicle truncate, lighter than rest of segment, bearing small, fine hairs, base with narrow, light band bearing small, fine hairs extending to lateral margins of segment (Fig. 164). Aedeagus capitate with posterodorsal lobe void of spinulae (Fig. 165D). Posterior sclerotized process bifurcate at base, projecting from posterior margin of lobe; dorsal arm forked at base-arm plate and at mid-length; arms of apical fork extending same length as base, pointed apically with sharp ventral spine (Figs. 165C & 168); small lobe bearing small, fine spinulae below insertion of sclerotized process (Fig. 165B), patch of small rounded spinulae on anterodorsal lobe (Fig. 165E); wide, dense band of small, stout spinulae covering mesal section (Fig. 165F), band of less dense, small, stout spinulae extending from mesal section to posterior margin (Fig. 165A).

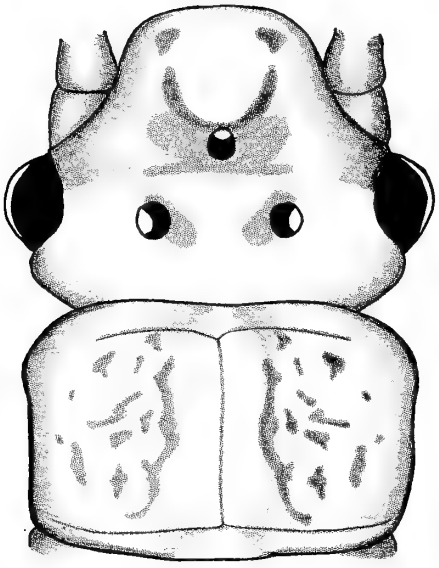
Female. — Macropterous. Length of forewings 8-11 mm; length of body 10-12 mm. General body color and head-pronotal pigment pattern similar to male. Subgenital plate broad at base, shallow, concave, median apical emargination, produced approximately 1/4 length of 9th sternum, lateral margins of base with variable medium-brown spot (Fig. 163).

Nymph. — Unknown.

Ova. — General shape oval, cross section circular (Fig. 193). Color medium-brown. Length .33 mm; width .25 mm. Collar absent; chorionic ridges elevated and thickened, forming irregularly shaped deep depressions, enclosing small punctations (difficult to observe due to depth of depressions) (Figs. 193-195). Micropyles set close together in pairs on top of ridges, near bottom 1/3 on one side (Fig. 196).

Material examined. — TYPES: Holotype ♂, OREGON: Union Co., 6 mi. E. of Medical Springs, Lick Crk., 23/VII/1975, DFTM Project (deposited at USNM),

FIGURES 162-168. — *I. bifurcata.* 162. adult head and pronotum (scale: 1 mm = .03 mm). 163. female subgenital plate (1 mm = .06 mm). 164. male vesicle and 8th sternum (1 mm = .44 mm). 165. male aedeagus, lateral aspect, A. band of small, stout spinulae, B. small posterior lobe bearing scattered small, fine spinulae, C. sclerotized process, D. large dorsal lobe, E. patch of small rounded spinulae, F. concentrated band of small, stout spinulae (1 mm = .02 mm). 166. male paraprocts, lateral aspect (1 mm = .02 mm). 167. male paraprocts, dorsal aspect (1 mm = .02 mm). 168. aedeagal sclerotized process (1 mm = .03 mm).



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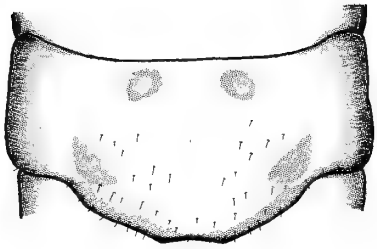

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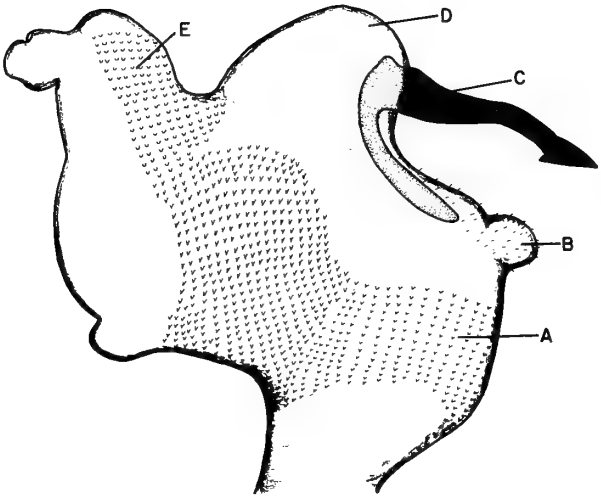

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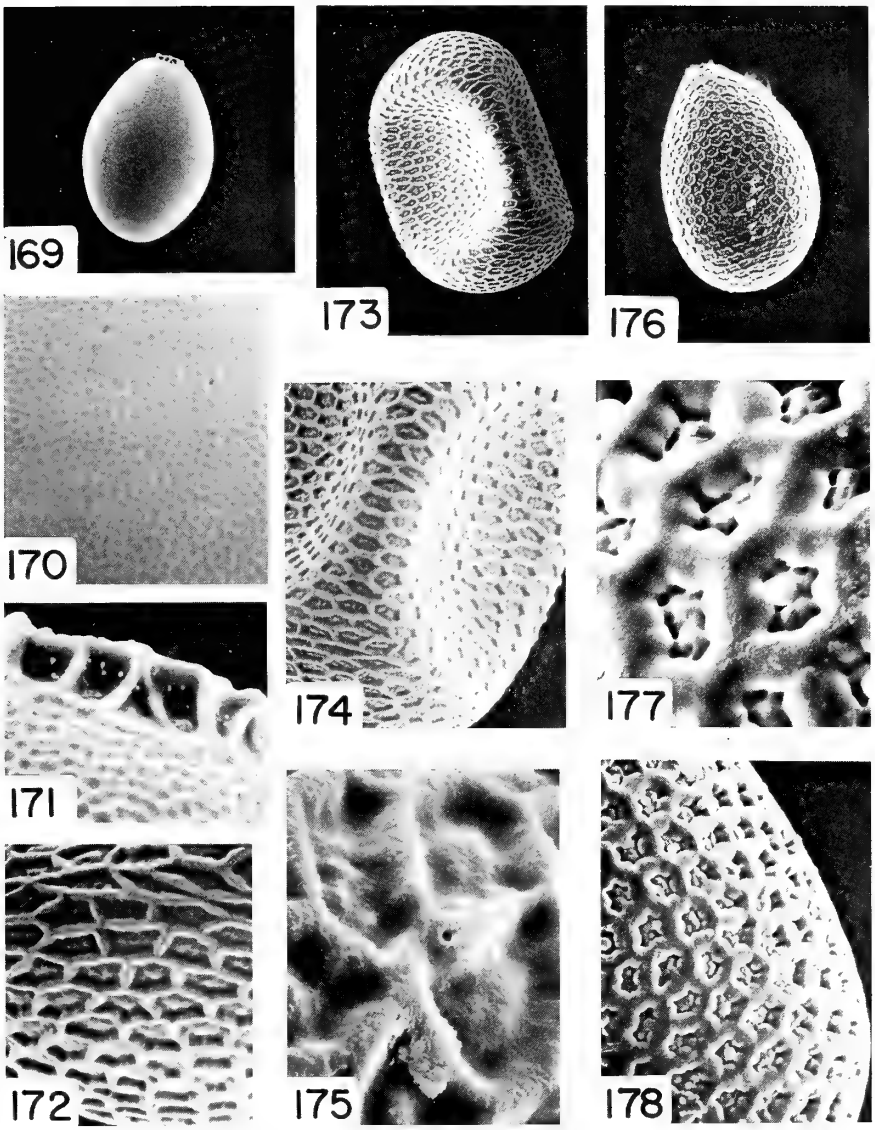
allotype ♀, 6 mi. E. of Medical Springs, Lick Crk., 30/VI/1976, DFTM Project (deposited at USNM). Paratypes, OREGON: Union Co., 6 mi. E. of Medical Springs, Lick Crk., DFTM Project, 1/VII/1975, 1 ♀, 9/VII/1975, 2 ♂, 2 ♀, 10/VII/1975, 1 ♀, 13/VII/1975, 3 ♂, 1 ♀, 14/VII/1975, 2 ♂, 3 ♀, 18/VII/1975, 25 ♂, 27 ♀, 22/VII/1975, 3 ♂, 3 ♀, 25/VII/1975, 2 ♂, 4 ♀, 28/VII/1975, 1 ♀, 29/VII/1975, 1/VIII/1975, 1 ♀, 5/VIII/1975, 1 ♀, 8/VIII/1975, 1 ♂, 12/VIII/1975, 1 ♀, 30/VI/1976, 5 ♂, 15 ♀, 2/VII/1976, 2 ♂, 13/VII/1976, 3 ♂, 1 ♀, 16/VII/1976, 4 ♂, 3 ♀, 29/VII/1976, 1 ♀, 30/VII/1976, 1 ♂ (paratypes deposited at USNM, SWS, NTSU, CWS, RWB, and SJ). Additional specimens — *USA* — CALIFORNIA: Trinity Co., Carryville, ?/VI/1913, E. C. Van Dyke, 4 ♂, 2 ♀ (CAS). IDAHO: Blaine Co., Galena, Hwy. 93, Horse Crk., near junct. OREGON: Clackamas Co., Mt. Hood, Hood R. Meadows, 31/VII/1948, K. M. Fender, 2 ♂, 4 ♀ (LCMNH), Mt. Hood, Still Crk., 15/VI/1947, S. G. Jewett, 1 ♂, 1 ♀ (LCMNH), Mt. Hood, Still Crk. Campground, 17/VI/1967, S. J. Jewett, 1 ♂, 1 ♀ (USNM), Swim, Still Crk., 15/VI/1947, S. G. Jewett, 1 ♂, 1 ♀ (LCMNH), Unknown Co., Olney, small crk., 8/VI/1940, S. G. Jewett, 3 ♂, 3 ♀ (UU). WASHINGTON: Pierce Co., Longmire, Mt. Rainier, 26/VII/1919, Fox, 1 ♀ (CAS).

Distribution. — USA: California, Idaho, Oregon, and Washington (Fig. 152).

Diagnosis and Discussion. — This species is most similar to *I. fusca.* Males can be distinguished by the truncate-shaped vesicle, stouter paraprocts, general spinulae pattern of the aedeagus, and aedeagal sclerotized process with shorter, stouter arms, not crossing and bearing a ventral spine at apex. Separation of females is difficult since the subgenital plate is very similar to *I. fusca* and *I. sordida.* In *I. sordida* the head pattern is much darker, with the interocellar area dark brown. The nymph of *I. bifurcata* is unknown. Ova can be differentiated by the much thicker, deeper chorionic ridges, irregularly shaped deep depressions, and absence of a collar.

Males and females from the type locality exhibited shorter wings than other populations examined, although body lengths were similar. In both males and females, the wings did not extend beyond the tip of the abdomen. The mean male and female wing lengths were 6.1 mm and 7.8 mm, respectively, compared to 9.1 mm and 10.0 mm from other populations. The head pattern of specimens from the type locality was also somewhat lighter than other populations, with no dark pigment band connecting the lateral ocelli to anterior ocellus; details of the male aedeagus and ova were identical in all populations.

This species has been confused with *I. sordida.* Gaufin et al. (1966) first illustrated the aedeagal sclerotized process under *I. sordida,* and this same illustration was repeated by Gaufin et al. (1972) and Baumann et al. (1977).



FIGURES 169-178. — Figs. 169-171. *I. denningi.* 169. whole ova 200×. 170. detail of chorion and micropyles 1000×. 171. detail of collar 2000×: Figs. 172-175. *I. adunca.* 172. detail of chorion, polar area 700×. 173. whole ova 200×. 174. detail of chorion mesal section 400×. 175. detail of micropyle 3000×: Figs. 176-178. *I. rainiera.* 176. whole ova 200×. 177. detail of chorion 2000×. 178. detail of chorion 700×.

Magnifications represent original values before reduction of plate.

No studies on the life history or general biology have been done. Emergence extends from late Jun. to mid-Aug. in small creeks.

Etymology. — This species name is derived from the double-forked dorsal arm of the sclerotized aedeagus process.

Isoperla denningi Jewett

Isoperla denningi, Jewett, 1955, 13:150. Holotype ♂, and allotype ♀; 4 mi. W. of Tanbark Flat, Los Angeles Co., California, USA (CAS) (male and female genitalia, and aedeagal structure).

Isoperla denningi, Illies, 1966:400.

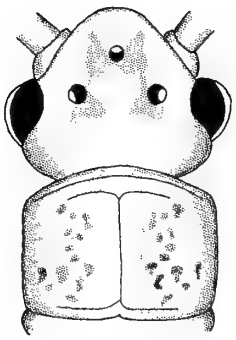
Additional references: *Isoperla denningi,* Jewett, 1960 (male and female genitalia, and aedeagal structure).

Male. — Macropterous. Length of forewings 9-11 mm. Length of body 9-10 mm. General body color light brown. Ocelli of head connected by narrow, dark brown, inverted "W"-shaped band of pigmentation; interocellar space light yellow (Fig. 179). Pronotum light brown, with median yellow stripe and small, rounded, dark brown rugosities (Fig. 179). Wings hyaline, veins light brown. Posterior margin of cercal segments with a long ventral hair. Vesicle parallel-sided, slightly constricted at base, expanded apically, darker than rest of segment (Fig. 184). Paraprocts broad at base, tapering to points at apex, recurving forward to level of 10th tergum (Fig. 182). Aedeagus with expanded dorsal lobe bearing concentrated, small, stout spinulae (Fig. 183D), posterior margin with sclerotized process, bifurcate at apex with arms of fork short, rounded at tips, base of process bifurcate (Figs. 181 & 183C), one small lobe below base of process bearing patch of small, fine spinulae (Fig. 183B); one large posteroventral lobe covered with concentrated, small, stout spinulae (Fig. 183A).

Female. — Macropterous. Length of forewings 11-13 mm; length of body 11-12 mm. General body color and head-pronotal pigment patterns similar to male. Subgenital plate broad at base, triangulate, median shallow emargination at apex, produced posteriorly over 1/2 9th sternum (Fig. 180).

Ova. — General shape oval, cross section circular (Fig. 169). Color light brown. Length .23 mm; width .17 mm. Collar slightly developed, with externally partitioned ridges (Figs. 169 & 171). Chorion covered with small, shallow, evenly spaced punctations, chorionic ridges absent (Figs. 169-171). Micropyles minute, arranged in pairs near bottom 1/3, on one side (Fig. 170).

Material examined. — TYPES: Holotype ♂, and allotype ♀, CALIFORNIA, Los Angeles Co., 4 mi. W. of Tanbark Flat, 21/VI/1950, H. L. Hansen (CAS). Paratypes, CALIFORNIA: Los Angeles Co., 4 mi. W. of Tanbark Flat, 21/VI/1950, H. L. Hansen, 1 ♀ (CAS), Angels Camp, 22/V/1930, E. P. Van Cuzee, 2 ♀ (CAS); Tuolumne Co., Keystone, 25/IV/1951, J. S. MacSwain, 1 ♂, 1 ♀ (CAS); Trinity Co., Carrville, elevation 2,400-2,500 feet, 19/V/1934, E. C. Van Dyke, 1 ♀ (CAS). Additional specimens — CALIFORNIA: Los Angeles Co., Brent's Mt., 20/V/1939, Collector ?, 2 ♂, 1 ♀ (LCMNH); Riverside Co., 2 mi. W. of Riverside, 17/V/1955, Collector ?, 2 ♂, 1 ♀ (RWB), Idyllwild, 18/VI/1952, M. Cazier, W. Gertach, and R. Schrammel, 2 ♂, 1 ♀ (SJ) Tehama Co., Salt, 11/V/1954, H. P. Chandler, 1 ♀ (CAS); Tuolumne Co., Keystone, 25/IV/1951, J. S. MacSwain, 1 ♂ (SJ).



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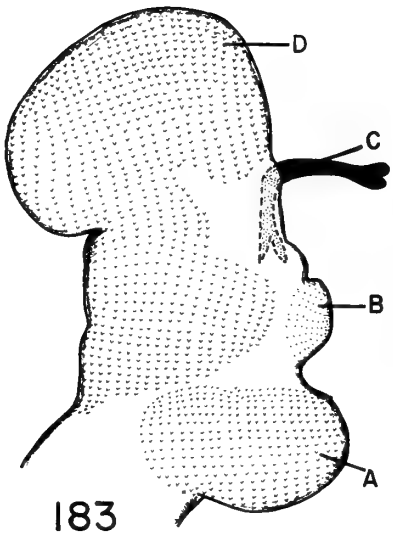

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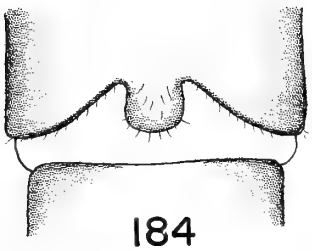

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FIGURES 179-184. — *I. denningi.* 179. adult head and pronotum (scale: 1 mm = .06 mm). 180. female subgenital plate (1 mm = .03 mm). 181. sclerotized aedeagal process, dorsal aspect (1 mm = .02 mm). 182. male paraproct, lateral aspect (1 mm = .02 mm). 183. male aedeagus, lateral aspect, A. large postero-ventral lobe, B. small posterior, bearing small, fine spinulae, C. sclerotized process, D. expanded dorsal lobe (1 mm = .01 mm). 184. male vesicle and 8th sternum (1 mm = .03 mm).

Distribution. — USA: California (Fig. 152).

Diagnosis and Discussion. — This species is closely related to *I. adunca.* Males can be distinguished by the light interocellar area of the head, darker wings and body, paraprocts wider at base and not deflected downward at apex, large expanded dorsal lobe on aedeagus bearing small, stout spinulae, sclerotized aedeagal process bifurcate at apex, and lack of long, sharp hair-like spinulae on proximal aedeagal stalk. Females can be differentiated by the light interocellar area of the head, darker wings and body, and generally wider, more angulate subgenital plate (in some specimens the subgenital plate is very similar). Nymphs of both species are unknown. Ova can be separated by the smaller size, circular cross section, developed collar, and lack of elevated chorionic ridges and hexagonal-shaped cells.

This is apparently a rare species, and no biological studies have been made. Emergence begins in late Apr. and continues until the end of Jun. in creeks.

Isoperla fusca Needham and Claassen

Isoperla fusca Needham and Claassen, 1925, 2:146. Holotype ♂, and allotype ♀; Waterton Lakes, Alberta, Canada (CNM) (male and female genitalia, and aedeagus).

Isoperla fusca, Claassen, 1940, 232:200.

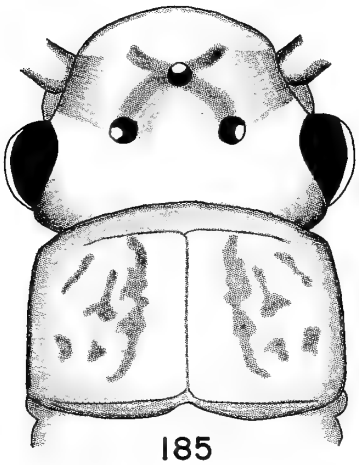
Isoperla fusca, Illies, 1966:403.

Isoperla fusca, Zwick, 1973:245.

Additional references: *Isoperla fusca,* Neave, 1929 (male aedeagus); Frison, 1942 (nymphal description, nymphal habitus, mandibles, maxillae, labrum, male and female genitalia, and adult head-pronotal pattern); Jewett, 1959 (male and female genitalia, and male aedeagus); Gaufin, 1964; Ricker, 1964; Knight et al., 1965 (ova); Gaufin, et al., 1966 (male and female genitalia, and sclerotized aedeagal process; Newell, 1970; Gaufin et al., 1972 (male and female genitalia, and sclerotized aedeagal process); Ricker and Scudder, 1975; Baumann et al., 1977 (male and female genitalia, and sclerotized aedeagal process).

Male. — Macropterous. Length of forewings 7.5-8.6 mm; length of body 7.0-8.1 mm. General body color blackish brown. Ocelli of head connected by narrow, inverted, "U"-shaped band of black pigmentation; symmetrical, shallow "U"-band

FIGURES 185-192. — *I. fusca.* 185. adult head and pronotum (scale: 1 mm = .04 mm). 186. nymph head, pro-, meso-, and metanota (1 mm = .06 mm). 187. male vesicle and 8th sternum (1 mm = .06 mm). 188. male paraproct, lateral aspect (1 mm = .02 mm). 189. sclerotized aedeagal process (1 mm = .03 mm). 190. nymph left hind leg (1 mm = .06 mm). 191. male aedeagus, lateral aspect, A. small posteroventral lobe, B. small mesoposterior lobe, C. sclerotized process, D. large conical anterodorsal lobe (1 mm = .04 mm). 192. female subgenital plate (1 mm = .03 mm).



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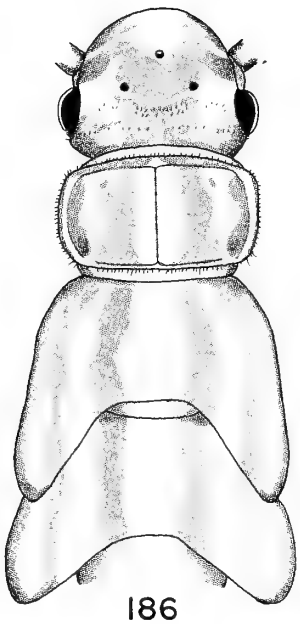

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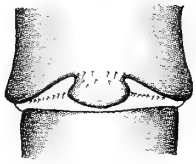

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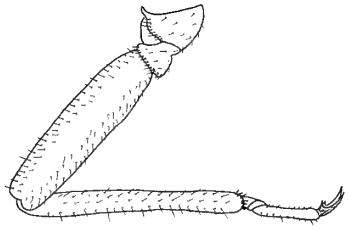

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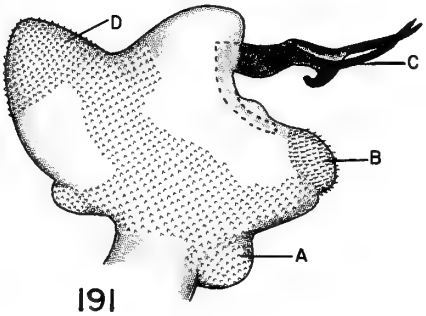

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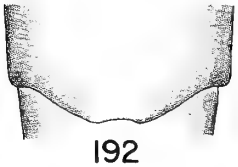

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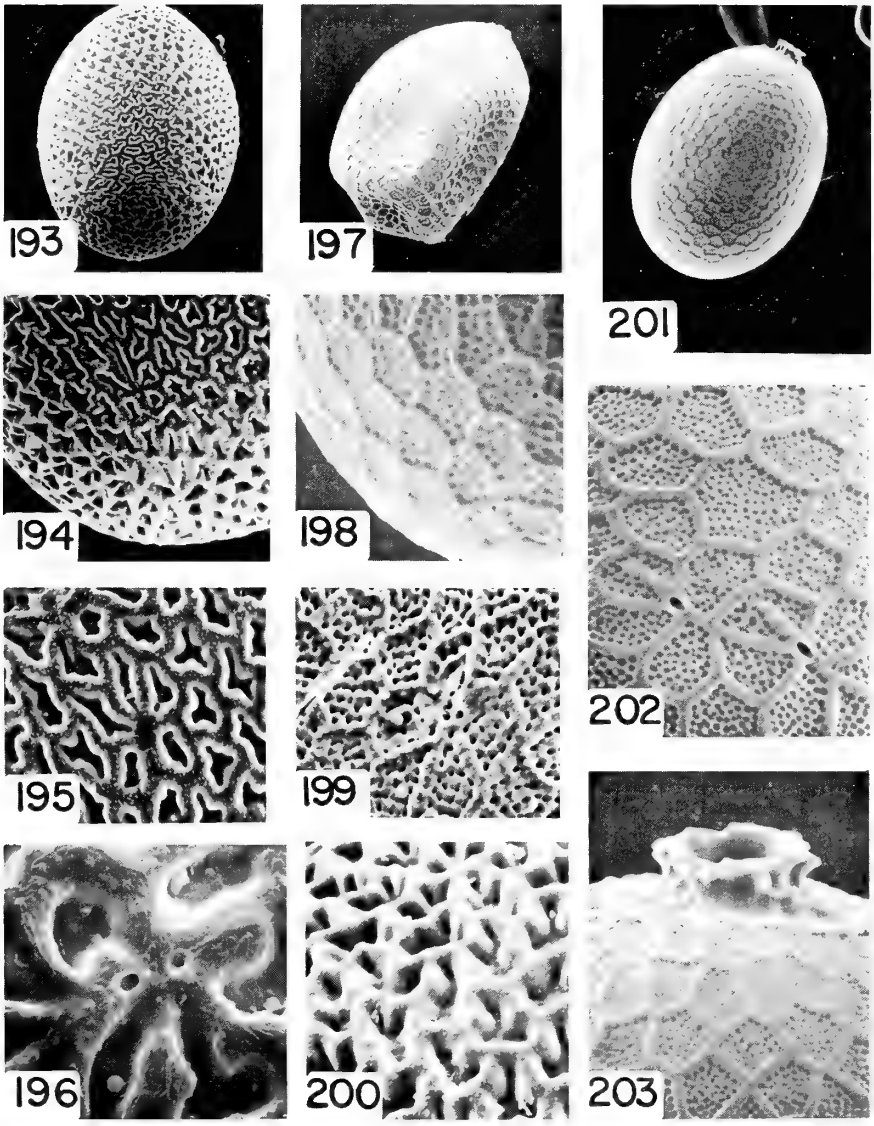
attached to inverted "U" at anterior ocellus; interocellar space light; wide, medium-brown band extending across head between bases of antennae (Fig. 185). Pronotum medium-brown, with median light stripe, rugosities black (Fig. 185). Wings hyaline, veins dark brown. Paraprocts short, tapering to points apically, covered with small, fine hairs, recurving anteriorly to level of 10th tergum (Fig. 188). Vesicle expanded at apex, evenly rounded posteriorly, lighter than rest of segment; few small, fine hairs at base (Fig. 187). Posterior margin of cercal segments with long ventral hair. Aedeagus with mesodorsal lobe void of spinulae, bearing posterior projecting sclerotized process, bifurcate at base; forked members of dorsal arm extending twice the length of base, tapering apically to long, fine points, crossed near apex; arms of forks bearing bent, finger-like ventral spine near 1/3 length (Fig. 191C); posterior lobe under projecting sclerotized process, covered with long, fine hair-like spinulae (Fig. 191B); small posteroventral lobe bearing small, stout spinulae (Fig. 191A); large, conical, anterodorsal lobe covered with small, stout spinulae (Fig. 191D); large patch of small, stout spinulae extending from anterodorsal lobe to posterior margin, rectangular patch void of spinulae below anterodorsal lobe.

Female. — Macropterous. Length of forewings 9.0-10.5 mm; length of body 9.0-11.0 mm. General body color and head-pronotal pigment patterns similar to male. Subgenital plate broad at base, evenly rounded posteriorly, with shallow median emargination, produced approximately 1/4 length of 9th sternum (Fig. 192).

Nymph. — Length of mature male nymph 7.8-9.6 mm; length of mature female nymph 9.6-10.6 mm. Interocellar area of head dark brown, with lateral arms extending to bases of antennae; broad, bowl-shaped brown pigmentation extending backward from near lateral ocelli; epicranial arms and stem a fine, "Y"-shaped light band; variable dark spots behind eyes; occipital ridge with a few scattered, small, fine spinulae (Fig. 186). Pronotum with median light stripe and 4 longitudinal dark brown bands; margin fringed with small, stout setae, occasional long hairs interspersed at upper and lower angles (Fig. 186). Meso- and metanota with 4 dark brown longitudinal band continuing from pronotal bands (Fig. 186). Outer surface of femora, tibiae and tarsi interspersed with spine-like setae, dorsal margins without typical fringe of long, fine hairs (Fig. 190). Abdominal terga with 3 longitudinal light stripes, one median and 2 lateral. Posterior margin of cercal segments with a whorl of small, stout setae.

Ova. — General shape oval (most appear crinkled due to alcohol preservation), cross section circular (Fig. 197). Color light brown. Length .30 mm; width .21 mm. Collar slightly developed (Fig. 197). Chorionic ridges elevated, forming hexagonal cells, each containing numerous, evenly spaced punctations (Figs. 197-199). Micropyles minute, arranged singularly on top of ridges near bottom 1/3, on one side (Fig. 199).

Material examined. — Paratypes; CANADA, Alberta, Waterton Lakes, 12/VII/1923, J. McDunnough, 2 ♂, 2 ♀ (CU #1,167). Additional specimens — *CANADA:* ALBERTA, Banff National Park, Lake Louise Crk., Lake Louise, 27/VII/1968, A. R. Gaufin, 3 ♂, 3 ♀ (RWB), Waterton Lakes, Kootenai R., 1/VIII/1970, A. R. Gaufin, 1 ♂ (UU). *USA* — IDAHO: Fremont Co., S. Fork of Fish Crk., N. of Warm R., 8/VII/1972, R. L. Newell, 1 ♂, 1 ♀ (RWB); Lemhi Co., crk. near Gibbonsville on Hwy. 93, 17/VI/1965, A. R. Gaufin, 1 ♂ (UU), Hwy. 93, S. of North Fork, Wagonhammer Springs, 17/VI/1965, A. R. Gaufin, 1 ♂, 2 ♀ (RWB). MONTANA: Beaverhead Co., Polaris Wise R. Road, Gold Crk., 7/VIII/1966, J. R. Grierson, 1 ♂ (UU); Carbon Co., 16 mi. W. of Red Lodge, W. fork Rock



FIGURES 193-203. — Figs. 193-196 & 200. *I. bifurcata.* 193. whole ova 200×. 194. detail of chorion 400×. 195. detail of chorion 700×. 196. detail of micropyle 2000×. 200. detail of chorion at pole and 1000×: Figs. 197-199. *I. fusca.* 197. whole ova 200×. 198. detail of chorion 400×. 199. detail of micropyle 1000×: Figs. 201-203. *I. sordida.* 201. whole ova 200×. 202. detail of chorion and micropyles 1000×. 203. detail of collar 1000×.

Magnifications represent original values before reduction of plates.

Crk., 29/VII/1966, J. R. Grierson, 1 ♂ (UU); Flathead Co., Birch Lake, 28/VII/1967, P. Milam, 2 ♂, 2 ♀ (UU), Birch Crk., 16/VII/1970, A. R. Gaufin, 1 ♂ (UU), Birch Lake, 10/VIII/1967, P. Milam, 3 ♂, 9 ♀ (UU); Glacier Co., small crk. near Rising Sun Information Point, Glacier National Park, 6/VII/1962, A. R. Gaufin, 102 nymphs (UU), Glacier National Park, Iceburg Lake, Iceburg Crk., 30/VII/1965, A. V. Nebeker, 1 nymph (UU), Glacier National Park, Two Medicine Lake, 31/VII/1965, A. R. Gaufin, 2 ♀ (UU), Glacier National Park, Rising Sun Crk., at St. Mary's Lake, 23/VI/1965, A. V. Nebeker, 8 nymphs (UU), Glacier Park, Iceburg Crk., 27/VII/1965, A. R. Gaufin, 4 nymphs (UU), Glacier Park, Belly R., 9/VII/1970, C. M. Yarmoloy, 1 ♂ (UU), Hwy. 89, Cutbank Crk., 22/VII/1966, A. R. Gaufin, 1 ♂ (UU), Glacier National Park, Trib. of Lake Mary, going to Rising Sun Observation Point, near ranger station, 6/VII/1967, A. R. Gaufin, 6 ♂ (RWB), small stream near Rising Sun Observation Point, 2/VII/1966, A. R. Gaufin, 3 ♂ (UU), 6/VII/1963, A. R. Gaufin, 3 ♂, 2 ♀ (UU), 6/VII/1962, A. R. Gaufin, 3 ♂, 1 ♀ (UU), 10/VII/1964, A. R. Gaufin, 8 ♂, 1 ♀ (UU), 9/VII/1964, A. R. Gaufin, 2 ♂ (UU), 29/VII/1970, A. R. Gaufin, 13 ♂, 15 ♀ (UU), 9/VII/1964, A. R. Gaufin, 1 ♂, 1 ♀ (UU), 18/VII/1965, A. R. Gaufin, 3 ♂, 2 ♀ (UU), near ranger station, Belly R., 3/VII/1970, C. M. Yarmoloy, 1 ♂ (UU), Glacier National Park, Fish Crk., 9/VII/1965, A. R. Gaufin, 3 ♂, 1 ♀ (UU), Glacier National Park, Trib. of Lake Mary, going to Rising Sun, near ranger station, 6/VII/1963, A. R. Gaufin, 3 ♂, 1 ♀ (RWB), Glacier National Park, Fish Crk. at junct. with McDonald Crk., 2/VII/1965, A. R. Gaufin and R. K. Allen, 2 ♂ (UU), Glacier National Park, Swift Current Lake, 17/VII/1965, A. R. Gaufin, 1 ♂ (UU), crk. 1/4 mi. N. of Babb, 3/VII/1965, A. R. Gaufin, 2 ♂, 1 ♀ (RWB), Hwy. 2, Glacier Park, Tunnel Crk., 12/VII/1963, Collector ?, 2 ♂ (UU), Glacier National Park, Many Glacier Campground, Webur Crk., 13/VII/1963, A. R. Gaufin, 1 ♂ (UU); Lake Co., Hwy. 32C, Lost Crk., 10/VII/1963, A. R. Gaufin, 3 ♂, 3 ♀ (UU); Meagher Co., Deeper, Sulpur Crk., 8/VII/1966, J. R. Grierson, 1 ♂ (UU); Missoula Co., Camp Crk., 23/VI/1967, A. R. Gaufin, 5 ♂, 10 ♀ (UU), W. of Lake Alva, Uhler Crk., 20/VI/1969, R. L. Newell, 1 ♂ (UU), Sawyer Crk., 23/VI/1967, A. R. Gaufin, 1 ♂ (UU), 6 mi. above Miller Crk., Little Pork Crk., 20/VII/1965, J. R. Grierson, 1 ♂ (UU); Powell Co., Monture Crk. Rd., McCabe Crk., 11/VII/1970, A. R. Gaufin, 1 ♂ (UU); Ravali Co., 17 mi. above Hwy. 93, Lost Horse Crk., 30/VII/1965, J. R. Grierson, 1 ♂ (UU), 2.6 mi. above Hwy. 93, Bear Crk., 12/VII/1965, J. R. Grierson, 1 ♂ (UU), 4.0 mi. above Black Bear ranger station, Daly Crk., 27/VII/1965, J. R. Grierson, 1 ♂, 1 ♀ (UU), 17 mi. above Hwy. 93, Lost Horse Crk., 30/VII/1965, J. R. Grierson, 2 ♀ (UU), Hwy. 93 N. of Victor, Big Crk., 18/VI/1965, A. R. Gaufin, 1 ♀ (UU), Florence, 3/VII/1912, Collector ?, 1 ♂ (CU), 15 mi. above Hwy. 93, Lost Horse Crk., 30/VII/1965, J. R. Grierson, 1 ♀ (UU); County ?, W. of McGregor, McGregor Crk., 1/VII/1967, A. R. Gaufin, 1 ♂ (UU); County ?, Kiowa, Cutbank R. and Tribs., 12/VII/1959, S. G. Jewett, 3 ♂, 2 ♀ (USNM). WASHINGTON: Pend Oreille Co., elevation 3,150 feet, Thomas Lake, Little Pend Oreille Lakes, 19/VI/1954, B. Malkin, 1 ♂ (SJ). WYOMING: Park Co., Yellowstone National Park, Dunraven Pass, Mt. Washburn, 2/VIII/1940, T. H. Frison and T. H. Frison, Jr., 4 ♂, 1 ♀, 2 nymphs, 1 exuvia (INHS).

Distribution. — CANADA: Alberta, British Columbia; USA: Idaho, Montana, Oregon, Washington, and Wyoming (Fig. 152).

Diagnosis and Discussion. — This species is closely related to *I. bifurcata* (see diagnosis and discussion under *I. bifurcata*), although ova characters are closer to *I. sordida*.

There is no detailed knowledge of the biology. Material examined was collected mid-Jun. to mid-Aug., and was most abundant in mid-Jul. Adults and nymphs were collected from small rivers and creeks.

Isoperla petersoni Needham and Christenson

Isoperla petersoni Needham and Christenson, 1927, 201. Type locality — Peterson's Spring, head of Logan R., Cache Co., Utah, USA (no type designation, habitus, adult male and nymph).

Isoperla fontium Neave, 1929, 4:161. Holotype ♂, and allotype ♀, Maligne Lake, Alberta, CANADA (CNM) (nymphal mandible, maxillae, male and female genitalia, and sclerotized aedeagal process). Syn. Ricker, 1954.

Isoperla petersoni, Needham (in Claassen), 1937, 69:81 designation of holotype ♂, and allotype ♀, Peterson's Spring, head of Logan R., Cache Co., Utah, USA (Cu #1,687) (male and female genitalia, aedeagus, and adult head-pronotal pattern).

Isoperla fontium, Claassen, 1940, 232:200.

Isoperla petersoni, Claassen, 1940, 232:204.

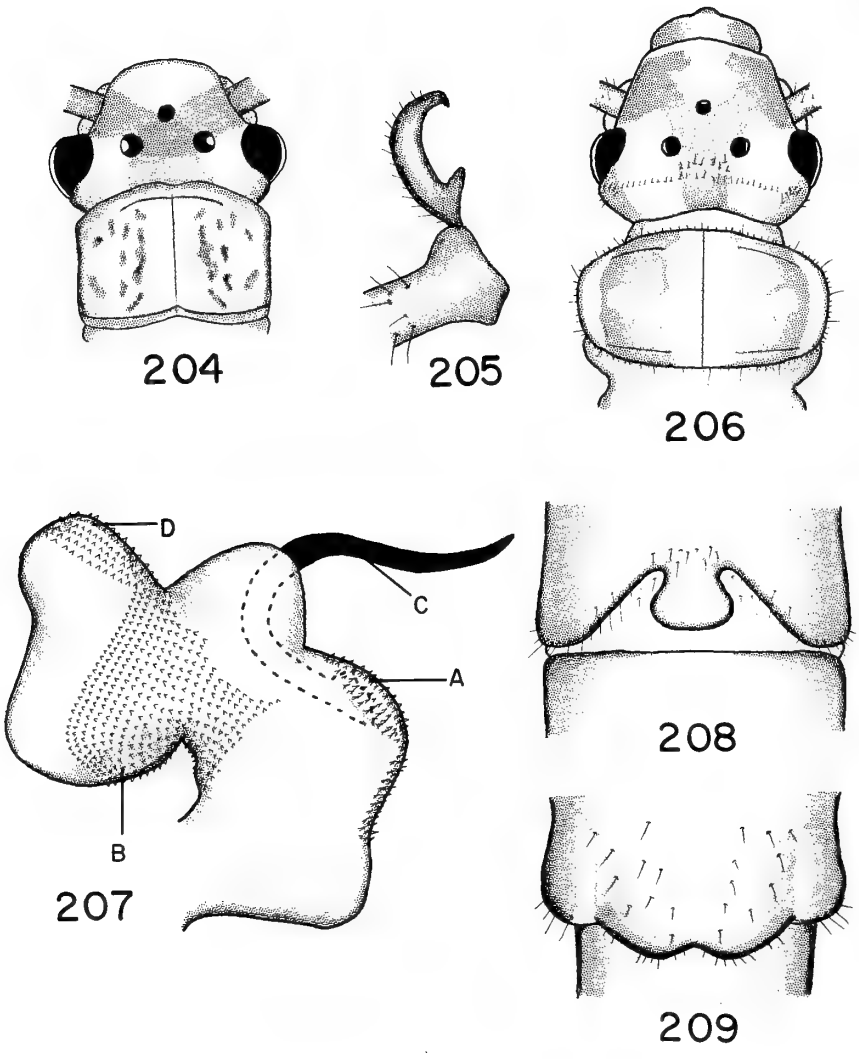
Isoperla petersoni, Ricker, 1954, 51:39. Syn. indicated.

Isoperla petersoni, Illies, 1966:415.

Isoperla petersoni, Zwick, 1973:250.

Additional references: *Isoperla petersoni,* Claassen, 1931 (nymphal habitus); Knowlton and Harmston, 1938; Jewett, 1959 (male genitalia and aedeagus); Ricker, 1964; Gaufin, 1964; Knight et al., 1965b (ova); Gaufin et al., 1966 (male and female genitalia, and sclerotized aedeagal process); Nebeker and Gaufin, 1966; Baumann, 1971; Gaufin et al., 1972 (male and female genitalia; and sclerotized aedeagal process); Ricker and Scudder, 1975; Baumann et al., 1977 (male and female genitalia, and sclerotized aedeagal process). *I. fontium,* Ricker, 1943 (adult head-pronotal pattern), 1944.

Male. — Macropterous-brachypterous. Length of forewings (macropterous) 9.0-10.5 mm; length of body 8.0-12.5 mm; length of forewings (brachypterous) 1.4-2.0 mm, length of body 7.5-9.5 mm. General body color dark brown. Interocellar area of head dark brown, forming equilateral triangle between ocelli; broad, diffuse brown "Y"-shaped band enclosing equilateral triangle and extending from base of antennae to occiput (Fig. 204). Pronotum medium brown, median light stripe, rugosities dark brown (Fig. 204). Wings fumose, veins dark brown. Long ventral hair at posterior margin of cercal segments. "C"-shaped paraprocts (laterally) stout, tapering slightly toward apex, apex blunt, distinctively deflected downward to a point, recurving anteriorly to level of 10th tergum, dorsal surface bearing small fine hairs; anterior tooth near base (Fig. 205). Vesicle constricted at base, posterior margin rounded, few small fine hairs at base, slightly lighter than rest of segment (Fig. 208). Aedeagus with mesodorsal conical-shaped lobe void of spinulae, bearing posterior projecting sclerotized process, bifurcate at base; dorsal arm developed into single long, curved, tapered, striolate, needle-like rod (Fig. 207C), patch of long, hair-like spinulae under process, continuing as narrow band down posterior margin (Fig.



FIGURES 204-209. — *I. petersoni.* 204. adult head and pronotum (scale: 1 mm = .06 mm). 205. male paraproct, lateral aspect (1 mm = .02 mm). 206. nymph head and pronotum (1 mm = .06 mm). 207. male aedeagus, lateral aspect, A. patch of long, hair-like spinulae, B. concentrated band of small, stout spinulae, C. sclerotized process, D. anterodorsal lobe (1 mm = .03 mm). 208. male vesicle and 8th sternum (1 mm = .03 mm). 209. female subgenital plate (1 mm = .03 mm).

207A); anterodorsal portion with rounded lobe bearing concentrated dorsal patch of large, stout spinulae (Fig. 207D); constricted area and posterior 1/2 of anteroventral lobe with dense band of small, stout spinulae (Fig. 207B).

Female. — Macropterous-brachypterous. Length of forewings (macropterous) 11-15 mm, length of body 10-15 mm; length of forewings (brachypterous) 3.0-5.5 mm, length of body 8-13 mm. General body color and head-pronotal pigment patterns similar to male. Subgenital plate evenly rounded posteriorly, with wide, shallow median emargination, produced 1/4 length of 9th sternum, long, stout hairs interspersed near base (Fig. 209).

Nymph (Reared). — Length of mature nymphs 9-12 mm. General body color medium brown. Dorsum of head with distinct medium brown band extending from occiput, covering interocellar area, and with lateral expanding arms extending to bases of antennae and forward, to near anterior margin of frons; light "U"-shaped area anterior to median ocellus, and 2 rectangular light areas mesad of eyes; occipital ridge bearing row of small, stout spinulae (Fig. 206). Pronotum light brown, median yellow stripe, 2 wide lateral brown bands, each enclosing light spot, rugosities absent; bordered by light margins; pronotum fringed with small, stout hairs and scattered longer hairs (Fig. 206). Femora, tibiae, and tarsi with scattered dorsal fringe of long, fine hairs, long, stout, spine-like setae interspersed on outer surface of femur, tibiae with row of medium-length stout, spine-like setae below dorsal fringe and at ventral margin. Abdominal terga with 3 light longitudinal stripes, one mesal and 2 lateral. Posterior margin of cercal segments with whorl of small, stout setae.

Ova. — General shape oval, cross section circular (Fig. 72). Color light brown. Length .29 mm; width .22 mm. Collar well developed, crown-shaped, sparse outer partitions ridges (Figs. 72 & 74). Chorionic ridges narrow, elevated, forming distinct hexagonal-shaped cells, each enclosing numerous, evenly spaced punctations (Figs. 72-74). Micropyles arranged in row of 2-5 on distinct, elevated, thickened transverse polar ridge near bottom 1/3, on one side (Fig. 73).

Material examined. — TYPES: *I. petersoni,* holotype ♂, and allotype ♀, *USA* — UTAH: Cache Co., Logan R., 17/VI/1926, J. G. Needham (CU #1,689). Paratypes, UTAH: Cache Co., Logan R., 26/VII/1926, J. G. Needham, 5 ♂, 1 ♀, 4 exuviae, 3 nymphs (CU #1,689). *I. fontium,* Paratypes, *CANADA* — ALBERTA: Maligne Lake, Date ?, Collector ?, 3 ♂, 2 ♀ (CU #1,168). Additional specimens — *CANADA:* ALBERTA, Forty Mile Crk., 19/VIII/1969, C. M. Yarmoloy, 7 ♂, 2 ♀ (UU), between Bow Falls and Spray R. junct., 18/VIII/1969, C. M. Yarmoloy, 6 ♂, 2 ♀ (UU & BS), above Bow Falls and Bow R., 19/VIII/1969, C. M. Yarmoloy, 3 ♂, 2 ♀ (UU), Banff, Marradine Lake, 18/VIII/1969, C. M. Yarmoloy, 8 ♂, 4 ♀ (RWB), Banff, above Bow Falls, 19/VIII/1969, C. M. Yarmoloy, 13 ♂, 4 ♀ (RWB). BRITISH COLUMBIA, Glacier National Park, below Fay Rock, 3/VIII/1961, J. Ricker, 1 ♂, 1 ♀ (WR), Glacier National Park, Incomappleux R. system, Freeze Crk., J. Ricker, 1 ♂, 1 ♀ (WR), Selkirk Mts., near Tangier Pass, 17/VIII/1961, J. Ricker, 1 ♂ (WR). SASKATCHEWAN, Hanson Lake Rd., stream entering Bow R., 21/VI/1974, L. Dosdall, 1 ♀ (US). *USA* — ALASKA: Anchorage jeep trap, Granite Crk., 8/IX/1966, K. N. Sommerman, 1 ♂ (USNM), Alaska N. Slope, Echooko R. Springs, 23/VII/1971, P. McCart, 4 ♂, 16 ♀ (WR). IDAHO: Fremont Co., Head Warm R., 19/VI/1955, S. G. Jewett, 13 ♂, 17 ♀ (SJ). MONTANA: Gallatin Co., Hwy. 191, bridge near Baconrind, W. Gallatin R., 26/VII/1963, A. R. Gaufin, 1 ♂ (UU); Glacier Co., Glacier National Park, Red Rock Falls, 28/VII/1970, A. R. Gaufin, 10 ♂, 15 ♀ (UU). UTAH: Cache

Co., Logan Canyon, Rick's Spring, 22/IX/1963, G. F. Knowlton, 13 ♂, 2 ♀ (UU), Logan Canyon, Rick's Spring, 29/VIII/1964, A. V. Nebeker, 7 ♂, 2 ♀, 9 exuviae (RWB), Logan Canyon, 24/IX/1939, W. P. Nye, 4 ♂, 2 ♀ (INHS), Logan Canyon, 29/X/1959, G. F. Knowlton, 1 ♂ (RWB), Logan Canyon, 21/IX/1961, G. F. Knowlton, 9 ♂ (BS), Logan Canyon, Utah Scout Camp, 17/IV/1938, D. E. Hardy, 18 ♂, 2 ♀ (RWB & INHS), Logan Canyon, Spring Hollow Crk., 9/XI/1963, A. V. Nebeker, 14 ♂, 3 ♀ (UU); Wasatch Co., Hwy. 40, above Strawberry Res., Trout Crk., Stat. 1, 23/VIII/1966, D. C. Hales, 3 ♂, 2 ♀ (RWB), 27/VII/1966, 1 ♀ (RWB), 6/VII/1966, 1 ♀ (RWB), 13/VIII/1966, 3 ♂, 2 ♀ (RWB), 15/IX/1964, 2 ♂, 4 ♀, 1 exuvia (RWB), 4/XI/1965, 1 ♂, 2 ♀ (UU), Stat. 2, 18/V/1965, 3 nymphs (UU), 20/VI/1965, 25 nymphs (UU), 7/VI/1965, 22 nymphs (UU), 8/VIII/1965, 16 nymphs (UU), 18/V/1965, 22 nymphs (UU), 12/I/1966, 24 nymphs (UU), 4/X/1966, 4 nymphs (UU), 6/VIII/1966, 6 nymphs (UU), 8/IX/1965, 2 nymphs (UU), 7/VI/1965, 4 nymphs (UU), 28/XII/1965, 3 nymphs (UU), 24/IV/1966, 15 nymphs (UU), 15/VI/1965, 3 nymphs (UU), 15/IX/1966, 1 nymph (UU), 20/VI/1965, 15 nymphs (UU), 13/VII/1966, 3 nymphs (UU), 18/III/1966, 25 nymphs (UU), 13/VII/1966, 7 nymphs (UU), 8/VIII/1965, 5 nymphs (UU), 4/X/1966, 7 nymphs (UU), 13/VII/1966, 5 nymphs (UU), 18/V/1965, 8 nymphs (UU), 14/V/1966, 27 nymphs (UU), 6/VIII/1966, 23 nymphs (UU), 20/VI/1965, 14 nymphs (UU), 7/VII/1965, 18 nymphs (UU), 23/VIII/1966, 12 nymphs (UU), 18/III/1966, 25 nymphs (UU), 3/IV/1965, 6 nymphs (UU). WYOMING: Teton Co., Grand Teton National Park, Cascade Canyon, 9/VIII/1940, T. H. Frison, 15 ♂ (INHS), Wilson, Coal Crk., 12/VIII/1940, T. H. Frison, 2 nymphs (INHS).

Distribution. — CANADA: Alberta, British Columbia; USA: Alaska, Idaho, Montana, Utah, and Wyoming (Fig. 152).

Diagnosis and Discussion. — This species is similar to *I. fusca.* Males can be distinguished by the completely dark interocellar area of the head, apex of paraprocts deflected downward and blunt at tips, and single, curved, needle-like sclerotized process of the aedeagus. Females can be differentiated by the completely dark interocellar area of the head, and narrower subgenital plate with scattered, stout setae (subgenital plates of *I. sordida, I. fusca,* and *I. petersoni* are very similar, and each species exhibits some variations in shape and presence or absence of a median emargination, making separation difficult at times). Nymphs can be separated by the continuous row of small, stout setae on occipital ridge, absence of 4 longitudinal dark bands on meso- and metanota, and presence of a scattered dorsal fringe of long, fine hairs on femora, tibiae, and tarsi. Ova can be distinguished by the presence of a well-developed collar and elevated, transverse micropyle ridge.

Authorship of this species has been confusing since its inception. Needham and Christenson (1927) reported that a new species had been collected from Peterson's Spring, Utah, and provided illustrations of the adult male and nymph, but no formal description or type designation was

given. They indicated that the species had been described by Claassen under the name *Isoperla petersoni*. Claassen (1931) described the nymph, and Needham, in Claassen (1937), provided a detailed description of male and female genitalia, including the sclerotized process of the aedeagus, and also designated the male holotype and allotype, and 21 male, 5 female, and many exuvial and nymphal paratypes from the Logan River, Utah. Authorship of this species has been assigned to Claassen (Claassen 1931), and to Needham (Claassen 1937), but in accordance with the International Code of Zoological Nomenclature, Needham and Christenson's mention of the species must be considered under the section "indications" of the Code, and they must therefore retain authorship as indicated by Ricker (1954).

I. petersoni exhibits varying degrees of wing length in both males and females. Populations in southern latitudes appear to have much shorter wings and slightly smaller bodies than those of more northern populations. A general increase in wing length was noted from Utah to British Columbia (Table 1). One population from Alaska exhibited shorter wings than other typically northern populations, but the specimens were collected from a spring, as were the Utah populations. It is thought that the more constant temperature regimes, characteristic of springs, probably alters wing length and nymphal development.

	♂		♀	
	$\bar{X}$ wing length mm range mm	$\bar{X}$ body length mm range mm	$\bar{X}$ wing length mm range mm	$\bar{X}$ body length mm range mm
Utah, Cache Co., Logan R.	1.6 1.5-1.9	8.1 7.2-8.7	3.1 2.7-3.3	9.0 8.3-9.2
Utah, Wasatch Co., Trout Crk.	1.7 1.4-2.0	8.3 7.7-9.3	4.1 2.9-5.4	11.5 9.4-12.6
Wyoming Teton Co., Grand Teton Nat'l Park	5.2 4.5-5.8	9.1 8.4-10.1	10.0 9.1-11.1	10.1 9.6-11.8
Idaho, Fremont W., Head of Warm R.	9.3 8.8-9.9	9.1 7.9-9.8	11.5 10.6-12.5	10.7 9.5-11.1
Montana, Glacier Co., Red Rock Falls	10.5 9.1-11.1	9.8 9.4-10.8	12.2 10.7-13.0	10.8 10.4-12.6
Alaska Echooka Springs	8.4 7.9-9.6	8.7 8.2-9.1	10.2 9.3-11.0	10.2 9.8-11.0
CANADA, Alberta, between Bow Falls and Spray R.	11.1 10.1-11.7	9.9 8.6-10.7	13.4 12.0-14.3	11.8 10.0-13.5
CANADA, British Columbia, Alberta Snowfield	11.6 10.8-12.3	10.8 9.8-12.6	14.7 14.2-15.0	13.4 11.4-14.6

TABLE I. — Varying wing lengths of *I. petersoni*.

Needham and Christenson (1927) reported that adults were collected on moss-covered stones near the water's edge, and that eggs were found suspended in gelatinous masses from stones in the water.

No life history or general biology studies have been done for this species. Based on the material examined, emergence occurs mid-Jun. to late Oct., and the species occurs in springs and small creeks.

Isoperla rainiera Jewett

Isoperla rainiera Jewett, 1954a, 11:549. Holotype ♂, Mount Rainier National Park, Pierce Co., Washington, USA (CWS) (male vesicle and aedeagal sclerotized process).

Isoperla rainiera, Jewett, 1962, 38:19. Allotype ♀, Trib. of Salmon R., Mt. Hood, Clackamas Co., Oregon, USA (CAS) (female genitalia).

Isoperla rainiera, Illies, 1966:417.

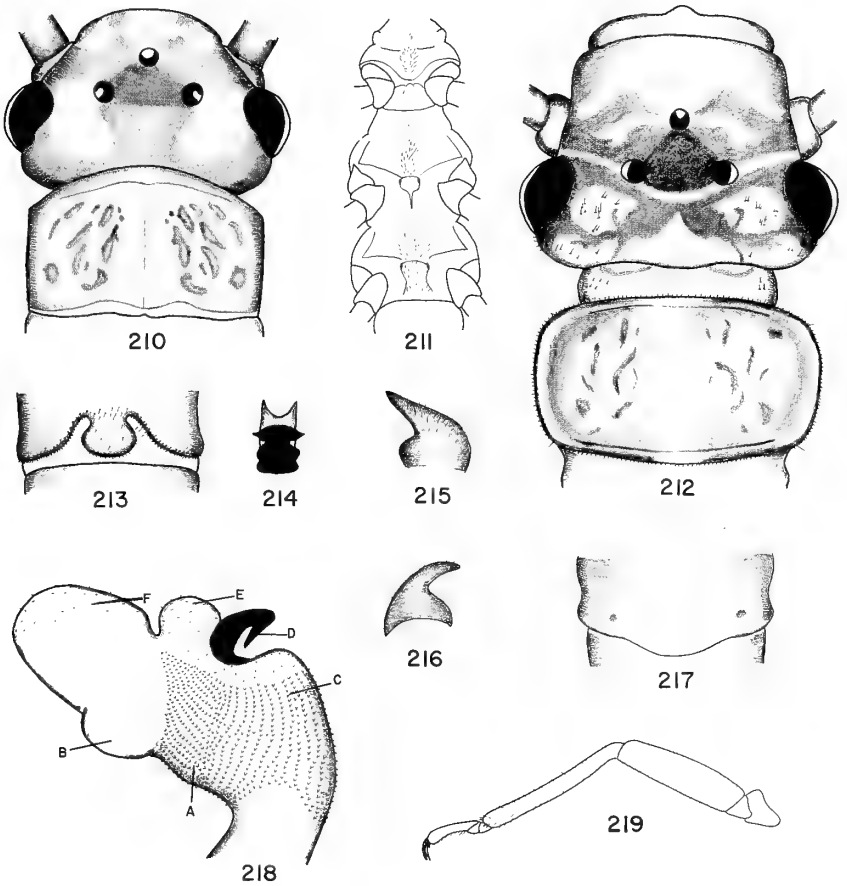
Additional references: *Isoperla rainiera,* Jewett, 1960 (aedeagal sclerotized process).

Male. — Macropterous. Length of forewings 8.5-9.0 mm; length of body 8.0-9.0 mm. General body color dark brown. Interocellar area of head completely dark brown, forming equilateral triangle between ocelli, diffuse, medium brown broad, "T"-shaped pigment band connecting bases of antennae and mesoposterior margin of head, enclosing ocellar triangle; two large light yellow spots between compound eyes (Fig. 210). Pronotum medium brown, light yellow median stripe, and numerous dark brown rugosities (Fig. 210). Dorsum of meso- and metathorax very dark. Antennae and legs dark brown, cerci light with long ventral hair at posterior margin. Wings fumose, veins dark brown. Abdominal terga with 8 faint rows of longitudinal dots, 2 mesal and 3 each laterally. Vesicle constricted at base, expanded at apex, evenly rounded at posterior margin, with few small, fine hairs (Fig. 213). Paraprocts wide at base, tapering to sharp, fine points apically, dorsoposterior surface bearing small, fine hairs; curved forward to level of 10th tergum (Figs. 215 & 216). Aedeagus tubular, posterodorsal sclerotized process with short bifurcate base, apex of dorsal arm expanded, evenly rounded, with 2 sharp, lateral downward deflecting spines (Figs. 214 & 218D); band of scattered, small, fine, hair-like spinulae on dorsal surface (Fig. 218F); large apical lobe, anteroventral margin with smaller lobe void of spinulae (Fig. 218B), small mesodorsal lobe anterior to sclerotized process bearing small, fine, hair-like spinulae (Fig. 218E); mesal section with band of small, rounded spinulae (Fig. 218A), and band of small, stout spinulae extending from posterior margin to mesal section (Fig. 218C).

Female. — Macropterous. Length of forewings 9.4-10.4 mm; length of body 9.0-10.9 mm. General body color and head-pronotal pigment patterns similar to male. Subgenital plate wide at base, evenly rounded posteriorly, produced approximately 1/4 length of 9th sternum (Fig. 217).

Nymph (Reared). — Length of mature male nymph 9.5-10.5 mm; length of mature female nymph 10.0-11.4 mm. Interocellar area of head dark brown, 2 light yellow areas inside and behind each compound eye, with scattered, long, fine hairs; posterior margin of head mostly light yellow, head pattern of numerous narrow black pigment bands (Fig. 212). Pronotum medium brown, broad median light yellow stripe, lateral rugosities dark brown; margin fringed with small, stout hairs, occasional long hairs at upper and lower angles (Fig. 212). Femora, tibiae, and

tarsi without typical dorsal fringe of long, fine hairs, outer surfaces with scattered, long, spine-like setae (Fig. 219). Pro-, meso-, and metathoracic sterna with median patch of long, golden brown setae, metasternal patch broadest (Fig. 211). Ventrum of abdomen cream yellow, dorsum mostly dark brown, with light, narrow median stripe. Cercal segments with whorl of short, stout hairs, and one long ventral hair at posterior margin.



FIGURES 210-219. — *I. rainiera.* 210. adult head and pronotum (scale: 1 mm = .06 mm). 211. nymphal thoracic sterna (1 mm = .08 mm). 212. nymph head and pronotum (1 mm = .07 mm). 213. male vesicle and 8th sternum (1 mm = .05 mm). 214. aedeagal sclerotized process (1 mm = .03 mm). 215. male paraproct, dorsal aspect (1 mm = .09 mm). 216. male paraproct, lateral aspect (1 mm = .09 mm). 217. female subgenital plate (1 mm = .02 mm). 218. male aedeagus, lateral aspect, A. mesal band of small, rounded spinulae, B. anteroventral lobe, C. wide band of small, stout spinulae, D. sclerotized process, E. small mesodorsal lobe, F. scattered band of small, fine, hair-like spinulae (1 mm = .03 mm). 219. nymphal left hind leg (1 mm = .09 mm).

Ova. — General shape oval, cross section circular (Fig. 176). Color medium brown. Length .30 mm; width .20 mm. Collar poorly developed (Fig. 176). Chorionic ridges elevated, thickened, forming obscured hexagonal-shaped depressions, with a number of small punctations (Figs. 176-178). Micropyles were not observed.

Material examined. — TYPES: Allotype ♀, *USA:* OREGON, Clackamas Co., Mt. Hood, Trib. of Salmon R., 14/VII/1956, S. G. Jewett (CAS). Additional specimens — *USA* — OREGON: Clackamas Co., Mt. Hood, Trib. of Salmon R., 9/VII/1955, 1 ♀, 38 nymphs (SJ), Mt. Hood, Trib. of Salmon R., 24/VI/1956, S. G. Jewett, 1 ♂, 1 ♀ (SJ), Mt. Hood, Trib. of Salmon R., 9/VII/1955, S. G. Jewett, 1 ♂ (RWB), Mt. Hood, Trib. of Salmon R., 23/VII/1955, S. G. Jewett, 2 ♂ (CAS), Mt. Hood, first crk., down from Timberline Lodge, on road to lodge, 31/V/1977, S. W. Szczytko and K. W. Stewart, 2 ♂, 5 ♀, 11 nymphs, and 1 exuvia (SWS & NTSU).

Distribution. — USA — Oregon and Washington (Fig. 152).

Diagnosis and Discussion. — This species is similar to *I. sordida.* Males can be distinguished by the pedicellate vesicle, shorter, stouter, paraprocts, general shape and smaller size of the aedeagal sclerotized process, and presence of small, rounded spinulae on mesal section of aedeagus. Females can be differentiated by the general darker body color and the slightly longer, more evenly rounded subgenital plate. The nymph of *I. sordida* is unknown, but *I. rainiera* nymphs can be separated from all other known species within the group by presence of the long, golden brown setae on the pro-, meso-, and metathoracic sterna, and the intricate dark head pattern. Ova can be distinguished by the poorly developed collar, thickened, elevated chorionic ridges forming hexagonal depressions, and lack of a micropyle ridge.

Nymphs of this species were successfully collected and reared from a small stream on Mt. Hood, Oregon. Nymphs were placed in styrofoam six-pac rearing chambers containing stream water, placed on ice and transported to Salt Lake City, Utah, via a commercial airlines flight. The rearing chambers were kept on ice while transported for 2 days by truck to Denton, Texas, and then maintained in an environmental chamber set at 8° C (approximating stream temperature). Adults began to emerge after one week in the environmental chamber. Two males and 5 females were reared, and remained alive for approximately one week.

No life history or general biology studies have been made for this species. Based on the material examined, emergence occurs early Jun. to mid-Jul. The species is apparently restricted to small, high mountain streams.

Isoperla sordida Banks

Isoperla sordida, Banks, 1906a, 38:337. Holotype ♂; Los Angeles Co., California, USA (MCZ #11,338) (male vesicle).

Isoperla sordida, Banks, 1907a:13.
Isoperla sordida, Claassen, 1940, 232:206.
Isoperla sordida, Illies, 1966:420.
Isoperla sordida, Zwick, 1973:251.
Additional references: *Isoperla sordida,* Needham and Claassen, 1925 (male and female genitalia); Hoppe, 1938; Jewett, 1956, 1959, and 1960 (male and female genitalia); Gaufin, 1946b (in part); Knight et al., 1965b (ova); Gaufin et al., 1966 (in part, male and female genitalia); Newell, 1970; Gaufin et al., 1972 (in part, male and female genitalia); Ricker and Scudder, 1975; Baumann et al., 1977 (in part, male and female genitalia).

Male. — Macropterous. Length of forewings 9.0-10.4 mm; length of body 9.0-10.0 mm. General body color dark brown. Interocellar space of head dark brown, forming equilateral triangle between ocelli, 2 hook-shaped, narrow, dark brown bands extending toward clypeus; medium brown triangular band connecting lateral ocelli to occiput; light brown band extending from interocellar triangle to base of antennae and front of eyes (Fig. 220). Pronotum light brown, median yellow stripe, numerous vermiform, dark brown rugosities (Fig. 220). Wings flavescent, veins dark brown. Abdominal terga with 8 faint rows of longitudinal dots, 2 mesal, and 3 each laterally. Paraprocts thin, elongate, tapering to long, fine points apically; small, fine hairs scattered on upper surface, recurving over 1/4 10th tergum (Fig. 223). Cerci with one long, fine ventral hair at posterior margin of each segment. Vesicle elongate, narrow at base, rounded at apex, lighter than rest of segment (Fig. 221). Aedeagus with large dorsal lobe void of spinulae (Fig. 225D), with stout sclerotized process; dorsal arm bifurcate at tip, apex of each arm rounded and bearing row of small, stout spines (Figs. 222, 225E, & 226); anterodorsal margin produced into large lobe with dorsal patch of small, stout spinulae (Fig. 225C), smaller ventral lobe void of spinulae (Fig. 225A), small median posterior lobe covered with small, stout spinulae (Fig. 225B); large patch of small, stout spinulae covering posterior and lateral aedeagus surfaces, extending along top half anterior lobe (Fig. 225C).

Female. — Macropterous. Length of forewings 10.5-13.1 mm; length of body 10.4-13.0 mm. General body color and head-pronotal pigment patterns similar to male. Subgenital plate indistinct, broad at base, evenly rounded posteriorly, with median shallow emargination, produced 1/4 length of 9th sternum (Fig. 224).

Nymph (described from female nymphal exuviae). — Length of mature female nymph 15-16 mm. Ocelli of head connected by band of dark brown pigmentation, band forming dark, equilateral triangle between ocelli, small light interocellar spot; wide, dark brown band extending from top of compound eyes and base of antennae to ocellar triangle; large "U"-shaped light area in front of anterior ocellus; occipital ridge bearing small, stout spinulae. Pronotum medium brown, median yellow stripe, 1 wide medium brown band, with variable light areas, bordering median stripe, margin fringe with short, stout setae, occasional long hairs interspersed at lower angles. Femora, tibiae, and tarsi with dorsal fringe of long, fine hairs, outer surface of femora with scattered spine-like setae, tibiae with ventral row of spine-like setae. Abdominal terga with 3 longitudinal stripes, 2 lateral and one mesal, and 8 faint rows of longitudinal dots, 2 mesal, and 3 each laterally. Posterior margin of cercal segments with whorl of small, stout hairs and one long ventral hair.

Ova. — General shape oval, cross section circular (Fig. 201). Color light brown. Length .32 mm; width .23 mm. Collar developed, expanded slightly at apex

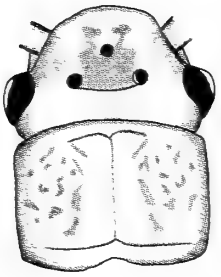
with elevated ridges (Figs. 201 & 203). Chorionic ridges elevated, forming hexagonal cells, each with numerous, evenly spaced, small punctations (Figs. 201-203). Micropyles arranged 2 or 4 on top of distinct, elevated, transverse polar ridge, extending through hexagonal cells near bottom 1/3, on one side; raised, elongate sperm guides below each micropyle (Fig. 202).

Material examined. — TYPES: *I. sordida,* Holotype ♂, *USA,* CALIFORNIA: Los Angeles Co., Date ?, Hutchinson (MCZ #11,338). Additional specimens — *USA* — CALIFORNIA: Los Angeles Co., L. Elizabeth Can., 26/IV/1950, Collector ?, 1 ♂, 1 ♀ (LCMNH); Trinity Co., E. C. Van Dyke, 2 ♂, 2 ♀ (CAS). MONTANA: Carbon Co., Rock Crk., Hell Roaring Crk., 29/VII/1966, J. R. Grierson, 1 ♂ (RWB); Glacier Co., Glacier Park, Siyeh Crk., 9/VIII/1963, Collector ?, 2 ♂ (RWB), Glacier Park, Siyeh Crk., 13/VIII/1963, Collector ?, 1 ♂, 1 ♀ (RWB), Waterton R., 23/VII/1970, C. Yarmoloy, 1 ♂ (RWB); Ravalli Co., 4.3 mi. above Hwy. 93, Chaffin Crk., 6/VII/1965, J. R. Grierson, 2 ♀ (UU), 1 mi. above Cameron Crk., Hart Crk., 23/VI/1965, J. R. Grierson, 1 ♂ (UU). OREGON: Deschutes Co., Fall R., 7/VI/1949, S. G. Jewett and Morton, 1 ♂, 1 ♀ (LCMNH), Fall R., 13/VII/1948, S. G. Jewett, 15 ♀, 10 nymphs (SJ); Jefferson Co., Wizard Falls, Metolius R., 19/IX/1949, L. E. Perry, 1 ♂, 1 ♀ (RWB), Wizard Falls, Metolius R., bridge near clear lake, 7/IX/1965, S. G. Jewett, 1 ♀ (USNM); Sherman Co., Sheep Bridge, Deschutes R., 16/IX/1948, S. G. Jewett, 6 ♀, 2 exuviae (CAS); Wallowa Co., Wallowa Mts., Lost Lake, 18/VIII/1952, K. M. Fender, 2 ♂, 2 ♀ (CAS), Crawfish Lake, trail above Anthony Lake, 12/VIII/1972, K. M. Fender, 1 ♂, 2 ♀ (CAS), Lake Crk. Camp, Lastine R., 19/VIII/1952, K. M. Fender, 3 ♂ (CAS).

Distribution. — CANADA: British Columbia; USA: California, Montana, Oregon and Washington (Fig. 152).

Diagnosis and Discussion. — *I. sordida* is closely related to *I. denningi.* Males can be distinguished by the completely dark interocellar area of the head, shorter, stouter, vesicle, longer, thinner, more acute paraprocts, longer, narrower sclerotized process of the aedeagus bearing short spines on apex of short, rounded arms, and lack of large dorsal expand aedeagus lobe covered with small, stout spinulae. Females can be differentiated by the completely dark interocellar area of the head, and much shallower, evenly rounded subgenital plate. The nymph of *I. denningi* is unknown. Ova can be distinguished by the large size, elevated chorionic ridges, elevated micropyle ridge, and raised sperm guides.

FIGURES 220-226. — *I. sordida.* 220. adult head and pronotum (scale: 1 mm = .09 mm). 221. male vesicle and 8th sternum (1 mm = .05 mm). 222. sclerotized aedeagal process, dorsal aspect (1 mm = .01 mm). 223. male paraproct, lateral aspect (1 mm = .03 mm). 224. female subgenital plate (1 mm = .05 mm). 225. male aedeagus, lateral aspect, A. anteroventral lobe, B. small mesoposterior lobe, C. patch of concentrated, small, stout spinulae, D. large dorsal lobe, E. sclerotized process (1 mm = .02 mm). 226. sclerotized aedeagal process, lateral aspect (1 mm = .001 mm).



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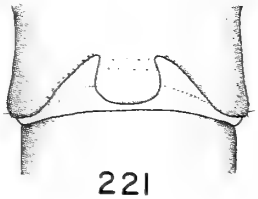

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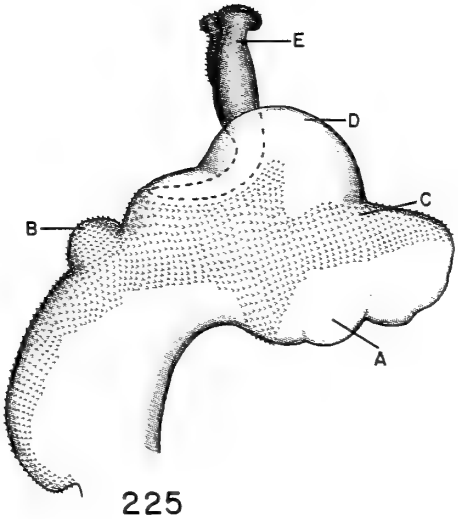

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There has been some confusion regarding the original generic placement of this species, and it has been incorrectly cited since its inception. Banks (1906a) originally placed the species in the genus *Isoperla*, although at that time he had grouped the *Isoperla* in the family Perlidae. In his catalogue (Banks 1907), it was cited as *Isoperla sordida* Banks (*Perla*), which was apparently an error. The sex of the type specimen has also been confused in the literature. The holotype in the Harvard collection is a male specimen, and the illustration (Fig. 5, ventral plate) in the original paper is the male vesicle of the 8th sternum, not the female subgenital plate.

This is a rare species, and no biological studies have been made. Based on the material examined, emergence occurs late-Apr. until early Sep., in creeks and small rivers.

Genus CASCADOPERLA NEW GENUS

Perla Hoppe, 1938, 4:151.
Isoperla Frison, 1942, 22:336.
Isoperla Illies, 1966:422.
Isoperla Zwick, 1973:252.

Type species. — *Isoperla trictura* (Hoppe), 1938, 4:151, herein designated.

Adult. — Body length: medium (8.0-11.5 mm). Wings: macropterous, hyaline, veins medium brown, venation typical for the genus *Isoperla*. Gills: absent from thorax or abdomen. Pronotum: median light stripe, bordered by 2 longitudinal dark brown bands. Mesosternum: arms of "Y"-shaped mesosternal ridge attached to posterior end of furcal pits, transverse ridge connecting anterior tips of furcal pits. Body color: yellow to light brown. Abdominal terga: 3 longitudinal dark stripes, 1 mesal and 2 lateral.

Male terminalia. — Ninth tergum: bipartite median patch of short, stout spinulae and dark pigmentation, mesoposterior margin elevated, with inverted "V"-shaped medium brown band. Tenth tergum: partial cleft extending from posterior margin, posterolateral margins of cleft developed into elongate, tapered, sclerotized genital hooks. Vesicle: absent. Paraprocts: joined at base, not connected to base of cerci, weakly sclerotized, blade-like, rounded at tips and produced 1/4 length over 10th tergum. Aedeagus: entirely membranous, tubular, bearing patches of small and long, hair-like spinulae.

Female terminalia. — Subgenital plate: reduced to a small median nipple on posterior margin of 8th sternum. Vagina: lined with small, stout spinulae, 7 long, tubular accessory receptacular glands attached to seminal receptacle; seminal receptacle a rounded, membranous sac.

Nymph. — Body length: medium (9.1-12.6 mm). Body color: light yellow. Pronotum: median light stripe, bordered by 2 wide, medium brown longitudinal bands, fringed with small stout hairs, numerous long hairs irregularly placed at upper and lower angles and posterior margin. Gills: absent from submentum,

thorax, and abdomen. Laciniae: apical and subapical teeth, subapical tooth ca. 3/4 length of apical tooth, bush of long, stout hairs on elevated, evenly rounded ridge below subapical tooth, 3 long, stout spines on inside margin below subapical tooth. Labrum: wide, evenly rounded median hump, lateral and anterior margins fringed with long, fine hairs. Mandibles: typical, as described for *Isoperla*. Labium: typical, as described for *Isoperla*. Mesosternum: typical, as described for *Isoperla*. Proventriculus: typical, as described for *Isoperla*. Abdominal terga: typical, as described for *Isoperla*.

Ova. — General shape: oval. Cross section: 9-sided polygon. Collar: well developed, expanded apically, forming large, flat top. Chorion: striate, 9 elevated longitudinal ridges, connected by lower transverse ridges, appearing ladder-like, forming large quadrangular-shaped pockets. Micropyles: arranged singularly on top of longitudinal ridges, near bottom 1/3 (Fig. 46).

Diagnosis and Discussion. — *Cascadoperla* is a monotypic genus. It shares the following characters with the *Isoperla:* 1. absence of gills or gill remnants on adult and nymphal thoracic and abdominal sterna; 2. fork of 2nd anal vein of forewings included in anal cell, so that its branches leave the cell separately; 3. arms of the "Y"-shaped mesosternal ridge in nymphs and adults attached to posterior end of furcal pits, and transverse ridge connecting anterior tips of furcal pits; 4. nymphal proventriculus with 26-27 longitudinal rows of sharp, posterior projecting spines; 5. 6-7 accessory receptacular glands attached to seminal receptacle or receptacular duct, vaginal floor with variable spinule patch; and 6. abdominal terga with 3 longitudinal stripes, 1 mesal and 2 lateral.

It differs from the *Isoperla* by the following characters: 1. posteromesal hump and bipartite patch of spinulae of the 9th tergum in adult males; 2. partial cleft and genital hooks of the 10th tergum; 3. lightly sclerotized, blade-like paraprocts, rounded at tips, contiguous at base and not connected to the base of cerci; 4. absence of vesicle from posteromedian margin of male 8th sternum (also absent in *I. ebria*); 5. reduced, nipple-like female subgenital plate on posteriomedian margin of 8th sternum; 6. presence of numerous, long, fine hairs on margin of the pronotum; 7. wide median hump on nymphal labrum; 8. bush of long, stout hairs and 3 long, stout spines on elevated ridge of nymphal laciniae; 9. continuous row of long dorsal and ventral hairs after 10th cercal segment; and 10. ova striate, with 9 longitudinal elevated ridges, connected by lower transverse ridges, forming large quadrangular pockets, each bearing numerous, minute punctations.

This genus is closely allied with *Calliperla* Banks, sharing lightly sclerotized paraprocts, genital hooks developed from posterior margin of 10th tergum, and spinule patch on posterior 1/2 of 9th tergum. It differs by the lack of supraanal process, absence of vesicle on 8th sternum, cleft

of 10th tergum, and greatly reduced subgenital plate. Both genera have retained characters of an *Isogenus* ancestor, such as the cleft and development of genital hooks from the posterior margin of the 10th tergum. These genera, plus the genus *Rickera* Jewett, probably represent transitory stages in the development and evolution of the *Isoperla* from *Isogenus*.

Cascadoperla is distributed throughout the Coastal and Cascade Mountain Ranges of the Pacific Coast, and also has limited distribution in the Northern Rocky Mountains of Idaho and Montana (Fig. 227). *Cas-*

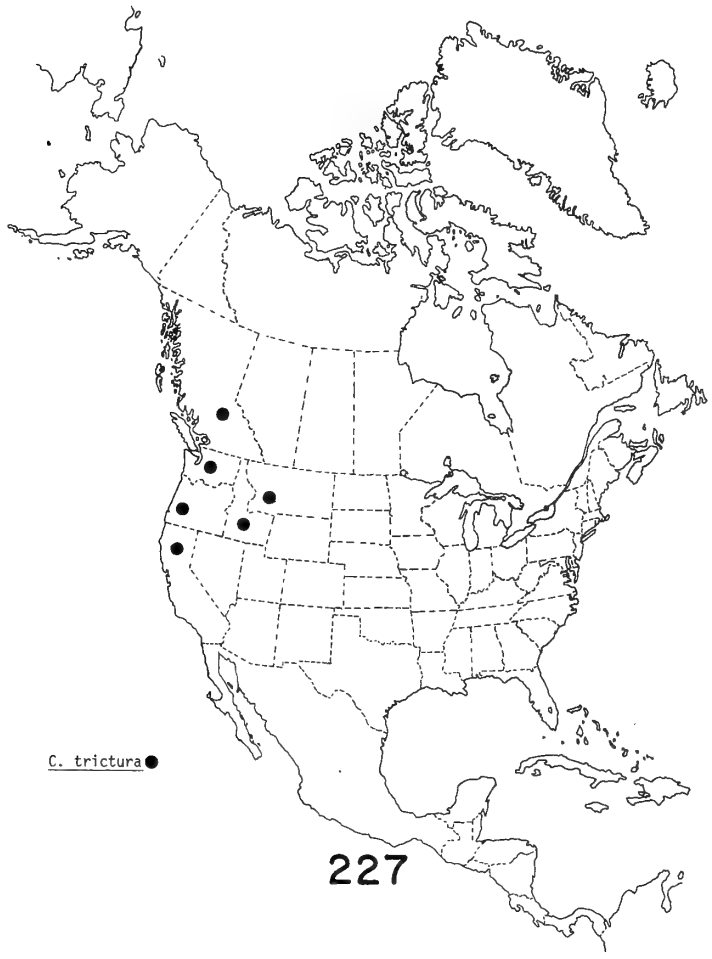


FIGURE 227. — Distribution of the genus *Cascadoperla*.

cadoperla trictura inhabits creeks and rivers, and emergence continues from mid-May until late Jul.

Etymology. — This genus name is taken from the Cascade Mountain Range of the Pacific Coast, where this species is quite abundant.

Cascadoperla trictura (Hoppe)

Perla trictura Hoppe, 1938, 4:151. Holotype ♂, and allotype ♀, Maple Valley, Cedar R., King Co., Washington, USA (TBM) (male and female genitalia).
Isoperla trictura, Frison, 1942, 22:336 (adult male head-pronotal pattern, and male and female genitalia).
Isoperla trictura, Illies, 1966:422.
Isoperla trictura, Zwick, 1973:252.
Additional references: *Isoperla trictura,* Ricker, 1943; Jewett, 1959 and 1960 (male and female genitalia); Gaufin, 1964; Knight et al., 1965b (ova); Gaufin et al., 1972 (male genitalia); Ricker and Scudder, 1975; Baumann et al., 1977 (male and female genitalia).

Male. — Macropterous. Length of forewings 8.0-9.5 mm; length of body 8.0-9.0 mm. General body color yellow to light brown. Round black spot covering interocellar area of head; wide medium brown band extending from occiput, through spot, and continuing to anterior margin of frons (Fig. 228). Pronotum light yellow, median light stripe bordered by 2 longitudinal dark brown bands containing vermiform rugosities (Fig. 228). Meso- and metanota dark brown, median light yellow stripe of pronotum extending 1/2 length of mesonotum. Wings hyaline, veins medium brown. Abdominal terga with 3 longitudinal dark brown stripes, one mesal and 2 lateral; 8 rows of longitudinal dots, 2 mesal and 3 each laterally. Ninth tergum with bipartite median patch of short, stout spinulae and dark pigmentation mesoposterior margin elevated, with inverted "V"-shaped medium brown band (Figs. 230 & 234). Tenth tergum with partial cleft, extending from posterior margin; posterolateral margins of cleft developed into elongate, tapered, sclerotized, genital hooks, appearing stout laterally, extending to anterior margin of segment (Figs. 230 & 234B). Posterior margin of cercal segments with a long ventral hair. Vesicle absent. Paraprocts joined at base, not connected to base of cerci, slightly sclerotized, rounded at tips, slightly tapered, dorsal surface bearing fine hairs, produced 1/4 length of 10th tergum just beyond base of genital hooks (Figs. 230 & 234A). Aedeagus completely membranous, tubular, nipple-like lobe at apex void of spinulae (Fig. 231D), anterodorsal section expanded slightly, bearing patch of concentrated, small spinulae extending to posterior base of nipple-like lobe (Fig. 231C), posterodorsal margin bearing concentrated patch of long, fine, hair-like spinulae, extending to mid-length and to anterior margin, below patch of small spinulae (Fig. 231B), proximal stalk void of spinulae except narrow band of very small, fine spinulae at posteroventral margin (Fig. 231A).

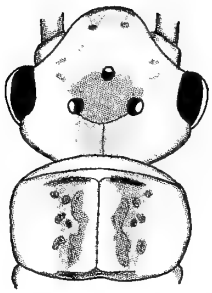
Female. — Macropterous. Length of forewings 9.5-11.0 mm; length of body 10.0-11.5 mm. General body color and head-pronotal pigment patterns similar to male. Subgenital plate reduced to small mesoposterior nipple on 8th sternum; darker than rest of segment; posterior margin of 8th sternum broadly rounded, with fringe of fine, medium-length hairs (Fig. 234).

Nymph (Reared). — Length of mature male nymph 9.1-10.3 mm; length of mature female nymph 10.2-12.6 mm. Interocellar area of head medium brown, wide, dark brown pigment band extending across frons; anterior margin with narrow, light transverse band, row of small, stout spinulae on occipital ridge (Fig. 229). Pronotal margin fringed with small, stout hairs, numerous long hairs irregularly placed at upper and lower angles and posterior margin; angles broadly rounded; median light yellow stripe bordered by 2 wide, medium brown longitudinal bands; rugosities absent; light narrow band on lateral and posterior margins (Fig. 229). Labrum with wide, evenly rounded median hump, lateral and anterior margins with fringe of long, fine hairs (Fig. 232). Laciniae with apical and subapical teeth; subapical tooth approximately 3/4 length of apical tooth; bush of long, stout hairs on elevated, evenly rounded ridge below subapical tooth; 3 stout spines on inside margin below subapical tooth (Fig. 233). Mandibles and labium typical, as described for western *Isoperla*. Proventriculus with 26-27 longitudinal rows of sharp posterior projecting spines. Femora, tibiae, and tarsi with dorsal fringe of long, fine hairs; ventral fringe of long, fine hairs on tibiae; scattered stout spines on outer surface of femora and tibiae. Abdominal terga with 3 longitudinal dark stripes, 1 narrow mesal and 2 wide lateral stripes. Posterior margin of cercal segments with whorl of small, stout setae, continuous rows of long dorsal and ventral hairs after 10th segment.

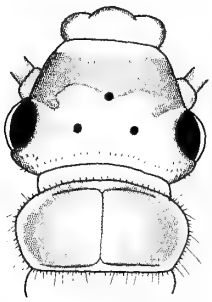
Ova. — General shape oval, cross section 9-sided polygon (Figs. 44 & 45). Color light brown. Length .30 mm; width .18 mm. Collar well developed, expanded apically, forming large flat top (Figs. 44, 45, & 50). Chorion striate, with 9 elevated, longitudinal ridges connected by lower transverse ridges, appearing ladder-like, forming large quadrangular-shaped pockets (Figs. 44-46). Micropyles arranged singularly on top of longitudinal ridges near bottom 1/3 (Fig. 46).

Material examined. — Paratypes, WASHINGTON: King Co., Maple Valley, Cedar R., 27/V/1973, G. N. Hoppe, 2 ♂ (INHS), Kittitas Co., Cle Elum, 15/VII/1932, G. N. Hoppe, 1 ♀ (INHS). Additional species — *CANADA* — BRITISH COLUMBIA: Vedder Crossing, 11-19/V/1937, W. Ricker, 2 ♂ (INHS), Cultus Lake, 12/V/1939, W. Ricker, 1 ♂, 1 ♀ (INHS), Cultus Lake, Lower Sweltzer Crk., 12/V/1937, W. Ricker, 8 ♂, 2 ♀ (WR), Cultus Lake, Chilliwack R., 8-22/V/1938, S. Spencer, 2 ♂ (INHS), Cultus Lake, Lower Sweltzer Crk., 12/IV/1941, W. Ricker, 8 ♂, 4 ♀ (INHS), Cultus Lake, Sweltzer Crk., 19/II/1939, W. Ricker, 22, 6 nymphs (INHS). *USA* — CALIFORNIA: Madera Co., Oakhurst, 26/V/1942, A. J. Watz, 1 ♂ (CAS); Yosemite Co., Yosemite Valley, 5/VII/1927, E. J. Nast, 1 ♂ (CAS). MONTANA: Ravalli Co., Hwy. 93, 1.5 mi. N. of Hamilton, Bitterroot R., 23/VII/1965, 2 ♀ (RWB). OREGON: Benton Co., 9 mi. N. of

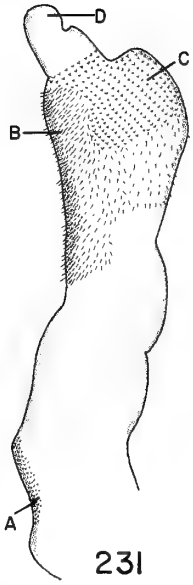
FIGURES 228-235. — *Cascadoperla trictura*. 228. adult head and pronotum (scale: 1 mm = .08 mm). 229. nymph head and pronotum (1 mm = .08 mm). 230. male terminalia, dorsal aspect (1 mm = .02 mm). 231. male aedeagus, lateral aspect, A. posteroventral band of small, fine spinulae, B. posterodorsal patch of long, fine, hair-like spinulae, D. dorsal nipple-like lobe (1 mm = .02 mm). 232. nymphal labrum (1 mm = .02 mm). 233. nymphal left maxilla, A. stipe, B. lacinia, C. apical tooth (1 mm = .03 mm). 234. male terminalia, lateral aspect, A. paraprocts, B. genital hooks, C. median bipartite spinulae patch of 9th tergum (1 mm = .02 mm). 235. female 8th sternum with mesoposterior nipple-like subgenital plate (1 mm = .04 mm).



228



229



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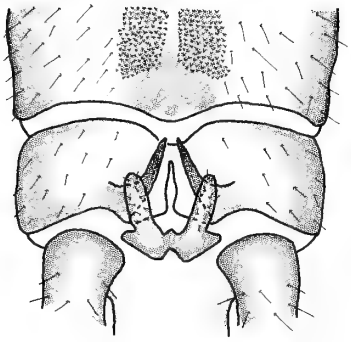

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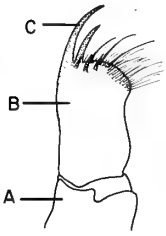

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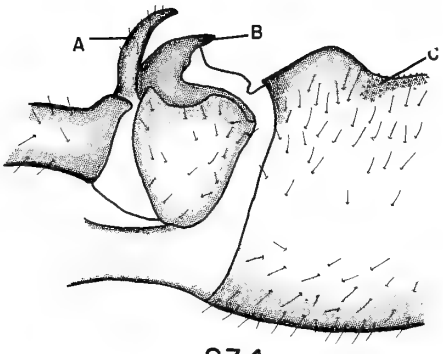

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Corvallis, Berry Crk., 16/V/1960, Collector ?, 1 ♂, 1 exuviae (SJ), Alsea R., 24/V/1939, Pillow, 1 ♀ (INHS), Hwy. 34 above Alsea, Rock Crk., 27/V/1977, S. W. Szczytko and K. W. Stewart, 4 ♂, 2 ♀, 1 nymph (SWS & NTSU), Oak Crk., 4/V/1934, E. E. Ball, 2 nymphs (INHS), Kings Valley Trib. of Luckiamute R., 11/V/1933, Prentiss and Dimick, 1 nymph (INHS); Clatsop Co., Necanicum R., 14/VI/1948, S. G. Jewett, 2 ♂ (BS), Youngs R., 10/V/1947, S. G. Jewett, 1 ♂ (OS[2]), Necanicum R., 13/VI/1948, S. G. Jewett, 3 ♂ (SGJ), Big Crk., 28/V/1949, S. G. Jewett, 35 ♂, 33 ♀ (SJ); Clackamas Co., Mollala R., 13/VI/1948, S. G. Jewett, 1 ♂ (INHS); Linn Co., Lacomb, Crabtree Crk., 4/VI/1935, R. Dimick, 1 ♂ (INHS); County ?, Willamette R., 26/V/1938, C. Jensen, 1 ♀ (INHS). WASHINGTON: Grays Harbor Co., Hamptulips, Hwy. 101, Hamptulips R., 18/VI/1967, R. W. Baumann, 1 ♂ (RWB); King Co., Cedar Falls, Cedar R., 22/VI/1972, J. Malick, 2 ♂, 2 ♀ (BS).

Distribution. — CANADA: British Columbia; USA: California, Idaho, Montana, Oregon, and Washington (Fig. 227).

Diagnosis and Distribution. — This species is distinctly unlike any described species of *Isoperla*. Males can be separated from all *Isoperla* by the head-pronotal pigment pattern, general yellowish body color, posteromesal hump of the 9th tergum, partial cleft of the 10th tergum and development of tapered sclerotized genital hooks from posterolateral margins of the cleft, lightly sclerotized paraprocts joined at the base, rounded at the tips and not connected to the base of the cerci, absence of a vesicle from the 8th sternum (also absent in *I. ebria*), and long, tubular aedeagus with apical nipple-like lobe. Females can be distinguished by the distinctive head-pronotal pigment pattern, general yellowish body color, and the reduced nipple-like subgenital plate. Nymphs can be separated by the distinctive head-pronotal pigment pattern, numerous long, fine hairs on the pronotum, wide, evenly rounded median hump of the labrum, bush of long, stout hairs on an elevated, evenly rounded ridge below subapical tooth of the laciniae, presence of 3 long, stout spines on inside margin below subapical tooth, and presence of a continuous row of long dorsal and ventral hairs after the 10th cercal segment. Ova can be distinguished by the deeply incised, striate chorion with 9 longitudinal ridges connected by lower, transverse ridges appearing ladder-like and forming large, quadrangular pockets, expanded apical section of the collar forming large, flat top, and by the numerous minute chorionic punctations.

The life history and general biology of this species are unknown. Based on the material examined, emergence occurs from mid-May until Jul. in creeks and rivers.

Discussion

This revision of the western Nearctic *Isoperla* provides a foundation for further analysis of the entire holarctic subfamily. Holomorphology of

the 21 western species has revealed 6 distinct morphological species complexes, unique in characters of the male aedeagus and ova.

The *I. quinquepunctata* complex (A) is thought to be the least specialized group, exhibiting an entirely membranous aedeagus, usually bearing tubular dorsal processes, patches of long, stout hairs or spinulae on the 9th and/or 10th male abdominal terga, and ova uniformly punctate without elevated chorionic ridges. *I. katmaiensis* is closely related, but was left unassigned to a group because of its unique unsculptured and ornate collared ova.

The *I. phalerata* complex (B) shows little additional specialization of the aedeagus, but the ova in both species have developed elevated chorionic ridges and enlarged micropyles, highly ornate and elevated in *I. pinta,* with multiple openings. The mebranous aedeagus and spinule patches on the male 9th tergum ally this group with the *I. quinquepunctata* complex and *I. katmaiensis.*

The *I. sobria* complex (C) exhibits intermediate specialization in aedeagal armature, and 2 of the species, *I. sobria* and *I. tilasqua,* bear patches of long, stout hair-like spinulae on the posterior margin of the aedeagus. The ova seem also to exhibit intermediate specialization, with elevated ridges forming hexagonal-shaped cells (absent in *I. sobria*), and well-developed collars. This complex is not closely related to any other, except *I. phalerata.*

The *I. marmorata* complex is further specialized, all species having an aedeagal sclerotized process and thickened chorionic ridges, forming irregular shaped depressions in the ova. The *I. sordida* complex represents the most advanced group and has the largest number of species. Further specialization is suggested by the highly modified, forked sclerotized aedeagal process, and variable ova characters. Several species (*I. adunca* and *I. bifurcata*) have collarless, ornate ova, and others (*I. petersoni* and *I. sordida*) have elevated, transverse micropyle ridges.

The Isoperlinae are closely related to, and probably developed from, the Perlodinae. Several primitive genera in the Isoperlinae, *Cascadoperla, Calliperla,* and *Rickera,* have retained important morphological features common in the Perlodinae, and represent transitory stages in the development and evolution of the *Isoperla.* In *Cascadoperla* the male terminalia are remarkably similar to most Perlodinae in that the 10th tergum is cleft and bears a pair of long genital hooks (10th tergum is uncleft in *Diura*). *Calliperla* has retained the epiproct of the Perlodinae (epiproct is absent in *Diura*) although it is short and unsclerotized, and in *Rickera* the male vesicle is located on the 7th abdominal sternum, which is common in all Perlodinae.

Isoperla therefore appears to be the most advanced genus in Isoperlinae, having lost typically Perlodinae characters, such as the cleft and genital hooks of the male 10th tergum, male epiproct, and movement of the male vesicle from the 7th to 8th abdominal sternum. A *Diura*-type ancestor is probable for *Isoperla,* but must remain a pertinent question until further holomorphological study of all genera of Perlodinae and Isoperlinae, as I have done for this 21-species western Nearctic *Isoperla* segment.

The Isoperlinae differ from the Perlodinae by the following characters: 1. 10th tergum entire (partially cleft in *Cascadoperla*); 2. genital hooks from 10th tergum absent (present in *Cascadoperla*); 3. paraprocts sclerotized and variously developed; 4. epiproct absent (present but weakly developed in *Calliperla*); 5. male vesicle present on 8th abdominal sternum (present on 7th sternum in *Rickera*); 6. ova usually round and sculptured (unsculptured in *I. katmaiensis*); 7. submental, thoracic, and abdominal gills absent; and 8. three longitudinal stripes on abdominal terga. These character differences are major, and if substantiated by further holomorphological study of the subfamily, they will undoubtedly prove of sufficient magnitude to justify return of the group to family status, as proposed by Frison (1942).

The male aedeagus, and ova, were found to contain the diagnostic characters for group and species separation. It is therefore suggested that collectors attempt to extrude aedeagii in male specimens at time of collections to facilitate identification. Ova were most useful in species separation but had limited use in separation of groups. Of course, SEM preparation is not always convenient or feasible for some field studies. Essentially, no substantive intra-species geographic variation was noted in the aedeagal characters of general shape, spinule patterns, shapes and sizes of spinulae, and presence or shapes of the sclerotized process, or the ova characters of size, shape, chorionic ridges and punctations, collar, and micropyle grouping and accessory structures (such as transverse ridges, elevated ornate structures, and sperm guides). Separation of females is difficult because of interspecific similarities of the subgenital plate and its great intraspecific variation. The presence, absence, or degree of the mesoposterior emargination was always a variable character in any population. Head and pronotal pigment patterns are the most reliable external characters, but their phylogenetic significance is obscure. The vagina was not diagnostic at the species or generic levels. All species exhibited 6-7 tubular accessory receptacular glands attached to the seminal receptacle or receptacular duct, vaginal cavity lined with variable spinulae, and the seminal receptacle membranous and variably shaped.

The wings offered little value for generic, group, or species separation. Vein variation was noted within and between populations. In several species, wing color was used to distinguish closely related species. It appears from this study that wing length is not a characteristic of the species, but rather of the environment.

Combinations of color patterns and setation of the cerci, legs, pronotum, and occipital ridge were used for differentiation of nymphs. The nymphal proventriculus was not diagnostic for species separation or for separation of *Isoperla* and *Cascadoperla*. All species possessed 23-26 variable longitudinal rows of stout posterior projecting spinulae. We were disappointed in the lack of inter-specific variation, and therefore diagnostic value, of the nymphal mouthparts of these western species, especially in light of great variation noted in eastern species we have studied (Szczytko and Stewart 1976, 1977, and 1978). Generic differences in the laciniae and labrum were diagnostic between the western *Isoperla* and *Cascadoperla*. The mesosternal ridge was consistent throughout all species, in that the arms of the "Y"-shaped ridge attached to the posterior end of the furcal pits and a transverse ridge connected the anterior tips of the pits.

Color patterns of the nymph and adults were useful in differentiating species, when used in combination with other characters. Some geographic variation was noted for each species, and striking color patterns of fresh material soon fade after a few years in preservative.

Data on the biology and life histories of these western *Isoperla* species is meager or nonexistent. This is surprising, since most species appear to be important, integral, functioning components of the benthic communities of western lotic systems (Fuller and Stewart 1977 and 1978; Stanford, unpublished Ph.D. dissertation). Data generated from such studies would also be useful in phylogenetic interpretations according to Henning's (1966) concept of holomorphology, and the importance placed on life history events patterns by Ross (1974).

This study involved 2 extensive field collecting trips, and examination of over 5,000 specimens from all available university, museum, and individual collections. However, several areas have received little collecting effort. Generally, specimens from Alaska, California, Northwest Territories, Washington, and the Yukon are poorly represented. These areas are very interesting from a zoogeographic and past dispersal standpoint, since they contain a number of endemic species, and may have been Pleistocene refugia (Ricker 1964). Of the 8 remaining undescribed nymphs, 6 are endemic to this region, and the other 2 are common. Future collection and rearing of these nymphs should receive high-priority

attention, enabling completion of the nymphal key and providing additional phylogenetic data.

I. katmaiensis is known only from the Alaskan Katmai Peninsula, and is probably an Alaskan refugium species. The primitive genera (*Cascadoperla, Calliperla,* and *Rickera*), and the more advanced *I. sordida* complex, are restricted mainly to the Pacific Coast, Cascade Ranges, with limited distribution in the Northern Rocky Mountains, suggesting they were derived from ancestors surviving the ice cover during the Pleistocene, below 48° N in those areas, or in the Alaskan refugium (Ricker 1964). Subsequent dispersal eastward into the northern Rockies have probably been along major river systems such as the Snake. *I. jewetti* is apparently a relict population or recently evolved species in stressed southern range limits (Texas and Colorado), and *I. longiseta* has successfully dispersed eastward into stressed grassland biome streams (Ricker 1964). The wide range of *I. longiseta* suggests a high vagility and wide tolerance to stress conditions. The remaining species are distributed from the Rocky Mountains to the Pacific Coastal Ranges in a wide variety of lotic habitats.

Summary

1. This holomorphological study of all life stages of western Nearctic stoneflies in the genus *Isoperla* was conducted over the 3-year period 1975-1978. Over 5,000 specimens from all available University, museum, and individual collections were studied.
2. An NSF Doctoral Dissertation Improvement Grant enabled two extensive field collecting-rearing trips during the seasonal emergence times of *Isoperla* in May, 1976 and May-Jun., 1977. Streams in New Mexico, Colorado, Wyoming, and Utah were collected in 1976. Different localities in these states were visited in 1977, and streams in the Coastal and Cascade Mountain ranges were collected in Oregon and Washington in 1977.
3. One monotypic genus new to science, *Cascadoperla,* is described, and *Cascadoperla trictura* (Hoppe) designated as the type species. The nymph, adult male and female, and ova are described and illustrated. Live nymphs were collected in Oregon in 1977, and successfully reared for the first time.
4. Three species new to science, *I. bifurcata, I. katmaiensis,* and *I. tilasqua* were discovered. Detailed descriptions are given for both adult sexes and the ova. *I. bifurcata* males and females were collected in Oregon in May, 1977.

5. The 21 species are arranged into 5 distinct complexes, and one unassigned species, primarily on the basis of male aedeagus and ova characters:

A. The *I. quinquepunctata* complex is composed of *I. jewetti* Szczytko and Stewart, *I. longiseta* Banks, *I. mormona* Banks, and *I. quinquepunctata* (Banks). All species share an entirely membranous aedeagus, usually bearing tubular dorsal processes, patches of long, stout hairs or spinulae on the 9th and/or 10th male abdominal terga, and ova uniformly punctate, without elevated chorionic ridges.

Unassigned — *I. katmaiensis* is closely related to the *I. quinquepunctata* complex. It is characterized by an entirely membranous aedeagus with 2 long, tubular dorsal processes, male 9th tergum with posterior bipartite patches of stout spinulae, and ova with non-sculptured chorion and ornate collar.

B. The *I. phalerata* complex is composed of *I. phalerata* (Needham) and *I. pinta* Frison. Its members are characterized by an entirely membranous, highly lobate aedeagus, male 9th tergum with either a single or bipartite patch of stout spinulae, male vesicle reduced, sharply tapered paraprocts with acute ventral spine, and ova with well-developed chorionic ridges and enlarged micropyles.

C. The *I. sobria* complex is composed of *I. sobria* (Hagen), *I. gravitans* (Needham and Claassen) and a new species *I. tilasqua.* Its members have an entirely membranous tubular aedeagus bearing one or more patches of long, hair-like spinulae, ova with developed chorionic ridges forming hexagonal-shaped cells, and large body size and dark pigment patterns.

D. The *I. marmorata* complex is composed of *I. fulva* Claassen and *I. marmorata* (Needham and Claassen). It is characterized by an aedeagus bearing a club-shaped sclerotized process, with small spines at the apex, broadly rounded, shallow male vesicle, and ova with elevated, thickened chorionic ridges forming irregular-shaped depressions.

E. The *I. sordida* complex is composed of *I. acula* Jewett, *I. adunca* Jewett, *I. denningi* Jewett, *I. fusca* Needham and Claassen, *I. petersoni* Needham and Christenson, *I. rainiera* Jewett, *I. sordida* Banks, and a new species *I. bifurcata.* They are characterized by a variably produced aedeagal process, forked at the base with a modified dorsal arm usually forked (not forked in *I. adunca, I. rainiera,* or *I. petersoni*), and ova usually with well-developed chorionic ridges (ridges absent in *I. denningi*) and variable collar (collar absent in *I. adunca* and *I. bifurcata*).

6. Six nymphal descriptions new to science are provided, with illustrations (nymph of *I. sordida* described from exuviae; no illustrations) including *I. longiseta, I. marmorata, I. mormona, I. phalerata, I. rainiera,* and *Cascadoperla trictura.* An example of rearing success was collection of *I. rainiera* nymphs from a snow-fringed stream at 1,867 m elevation on Mt. Hood, Oregon, successful transport to Texas, and rearing of 5 individuals in an environmental chamber.
7. Complete descriptions of ova, with accompanying SEM photographs, are provided for 20 species of *Isoperla* (females and ova are unknown for *I. acula*), and the one species of *Cascadoperla.* Eleven of these are described for the first time.
8. Two species are placed in synonymy. *I. patricia* was found to be a synonym of *I. quinquepunctata* (Banks), based on similarities of adult and nymphal pigment patterns and other shared characters, especially the ova and aedeagii. Detailed comparisons were made of ova from both types, and of the aedeagii from the *I. patricia* holotype and *I. quinquepunctata* males from near the type locality.

   I. ebria (Hagen) is placed in synonymy with *I. sobria* (Hagen), based on similarity of the female genitalia and ova. Ova from both types were identical.
9. Keys based on comparative morphology are provided for all known males, females, ova, and nymphs of *Isoperla* and *Cascadoperla.*
10. Two hundred thirty-five original illustrations, including SEM photographs, are presented.

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ROWLAND M. SHELLEY

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REVISION OF THE MILLIPED GENUS *SIGMORIA* (POLYDESMIDA: XYSTODESMIDAE)

BY

ROWLAND M. SHELLEY[1]

INTRODUCTION

The southern Appalachian Mountains of western North Carolina and adjacent areas are one of the prime global centers of milliped evolution and the major area of concentration of the Xystodesmidae, the dominant Nearctic polydesmoid family (Hoffman 1969). Most xystodesmids, especially representatives of the tribe Apheloriini, display vivid dorsal color patterns, and south of the Nolichucky River the dominant forms are black with red paranota and reddish, white, or bluish stripes along the caudal margins of the metaterga. This striped color pattern is also displayed by xystodesmids outside the Appalachians, occurring in animals that range south and east into the Atlantic and Gulf Coastal Plains, and west into the Cumberland Plateau. Four genera — *Sigmoria, Sigiria, Falloria,* and *Hubroria* — have been erected for these striped xystodesmids, but the distinctions between them are unclear, suggesting that some or all of the names might be synonymous. As noted by Shelley (1977a), no attempts have been made to define limits for these genera, and the problem is especially acute for the first two, proposed consecutively by Chamberlin (1939). All four taxa refer to forms in which the telopodite of the male gonopod curves in a vaguely sigmoid fashion, and all were poorly diagnosed. Several additional, undescribed "sigmoid" xystodesmid genera occur in

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the southern Appalachians and southeastern United States, but it would be imprudent to diagnose them until the established ones are clarified. Hoffman (1950a) summarized the genus *Sigmoria,* but the only revisionary effort to date in any of the four genera is that of Shelley (1976) on the *Sigmoria latior* (Brolemann) complex. This, however, did not address difficulties at the generic level. Inability to correctly allocate "sigmoid" xystodesmids to genera is thus one of the most vexing problems in the taxonomy of Nearctic diplopods, and resolution of the difficulties with *Sigmoria, Sigiria, Falloria,* and *Hubroria* is imperative if we are ever to gain substantial knowledge of this fauna, not only systematically but ecologically, physiologically, and ethologically as well.

My investigations on this enigma have been in progress for over five years. The work was severely hampered at the outset by the Chamberlinian descriptions and illustrations, always a problem but especially troublesome here due to the complexity of this particular fauna. Moreover, the holotype of *Sigmoria munda* Chamberlin was unavailable until 1978, and since this is the type species of *Sigmoria,* which would have priority over all the other generic names in case of synonymies, the status of all four taxa could not be determined until this specimen was examined. I tried several times to collect topotypes of *munda* without success.

The main obstacle to my investigation, however, was the absence of preserved study material from vast areas of the ranges of these four genera, and a major field effort was clearly essential. Obvious similarities between the many different "sigmoid" forms of the southeastern United States indicated that the entire relevant fauna of this region would have to be assembled, and the generic concepts reevaluated. Consequently, a comprehensive milliped collecting program, believed to be the most thorough ever undertaken in North America, was launched, emphasizing the southern Blue Ridge and Ridge and Valley Physiographic Provinces. Peripheral areas known to harbor related forms were also investigated, in the Cumberland Plateau of central Tennessee and Alabama, the Coastal Plain of Georgia and South Carolina, and peninsular Florida. Collections in major museums of the eastern United States also were examined for pertinent material. As a result of this effort it seems reasonable to conclude that at least 90% of the pertinent forms have been secured and that a synthesis may now be profitably attempted. A few highly localized endemics may have escaped detection, perhaps in remote areas of the Great Smoky Mountains National Park or similar places, but such species likely will not fundamentally alter generic concepts and can be described later.

Since it is the oldest pertinent generic name, having been proposed by Chamberlin (1939) two pages ahead of *Sigiria, Sigmoria* is valid for this genus and is retained as the senior synonym of both *Sigiria* and *Falloria*. *Sigiria,* relegated without explanation to synonymy under *Sigmoria* by Hoffman (1979), actually does belong there, although some forms previously referred to *Sigiria* display subtle differences from the type species of *Sigmoria*. The acropodites of the gonopods of the type species of *Sigiria,* for example, are essentially coplanar, the arch is high and gently curved at the "peak" (see terminology section under gonopodal taxonomic characters) so that the acropodite extends only to the level of the prefemoral process in medial view, and the medial flange is located mostly on the "distal zone." In the type species of *Sigmoria* the acropodite curves through more than one vertical plane, is flattened at the peak so that the arch overhangs and extends beyond the level of the prefemoral process in medial view, and the medial flange is located on the proximal portion of the peak. However, these differences are not invariably maintained by all relevant forms; for example some which have the medial flange on the distal zone, a trait of *Sigiria,* also possess a flattened peak which overhangs the prefemoral process, a trait of *Sigmoria*. The location of the medial flange is the only consistently different feature between *Sigmoria* and *Sigiria,* but even this appears to have an exception. *Sigmoria leucostriata* n. sp. has a small *Sigmoria*-like medial flange on the proximal portion of the peak and small medial and lateral lobes on the distal zone where the flanges of *Sigiria* are located (Fig. 84). I believe that these lobes represent greatly reduced *Sigiria* flanges and that *leucostriata* can be interpreted as possessing features of both nominal genera. Moreover, the geographic location of *leucostriata,* adjacent to the range of the type species of *Sigiria,* is precisely where one would expect to find an intermediate form displaying characters of two ostensibly different taxa. Thus, no single character or combination of characters exists which will distinguish *Sigiria* from *Sigmoria,* and I therefore agree with Hoffman's action (1979) in placing the former in synonymy. The monotypic genus *Falloria* is based on a species displaying obvious gonopodal similarities to the type species of *Sigmoria,* and is therefore placed in synonymy herein. Commentary on the fourth established "sigmoid" genus, *Hubroria,* will be presented in another paper. Proposed by Keeton (1960), *Hubroria,* currently monotypic, appears to be valid and refers to "sigmoid" forms in the Cumberland Mountains of Tennessee and the southeastern Coastal Plain. However, more material is needed before it can be adequately treated.

In addition to these generic changes, some shifting of species is necessary to create homogeneous groupings (Hoffman 1958). Consequently, *houstoni* Chamberlin and *mimetica* (Chamberlin) must be removed from *Sigmoria* and left temporarily unassigned. I agree with Keeton (1965), who returned *Sigmoria evides* (Bollman) to *Fontaria,* but the action of Hoffman (1967), in placing *Sigmoria divergens* Chamberlin and *nigrescens* Hoffman in *Cleptoria,* should be reviewed in light of the concept of *Sigmoria* presented herein. These forms hardly seem congeneric with the type of *Cleptoria, C. macra* Chamberlin, and may need to be returned to *Sigmoria* or placed in a new, monotypic genus. *Sigmoria gracilipes* Chamberlin was recently moved to *Brachoria* (Shelley 1979a) because of the distinct cingulum on the gonopodal acropodite, visible in Chamberlin's illustration (1947). In the present paper *mariona, brachygon,* and *zyga,* all authored by Chamberlin, are assigned to synonymies since they are based on forms with older names; *intermedia* (Hoffman) is reduced to a subspecies of *nigrimontis* (Chamberlin), which was proposed one year earlier; and a nomenclatorial change is made within the *latior* complex. Finally, 17 new species and 3 new subspecies were discovered in field sampling, bringing the composition of *Sigmoria* to 22 species, 3 of which are divided into a total of 9 subspecies.

The complexity of the southeastern apheloriine fauna and the necessity of collecting as many "sigmoid" forms as possible created two major problems in the course of this project. At first I experienced difficulty securing material in areas where the millipeds occurred, and I eventually realized that most of the montane species inhabit a very precise and readily definable environment. These forms occur exclusively in cool, moist coves or similar habitats along streams. I never found more than one species at a given site, and the animals may occupy the same or very similar niches. These diplopods are referred to as "cove inhabitants," to distinguish them from forms occurring in general, climax or subclimax, deciduous forests. Details of the cove environments and a discussion of ecological preferences of all species are presented in the ecology section.

The second problem concerned determining affinities among the 22 species of *Sigmoria* and how to best present this information in a publication. The chosen approach divides the fauna into 10 species groups based on a combination of anatomical similarities (mostly involving male gonopods) and geographical proximity. I think that the *latior, simplex, quadrata, leucostriata, rubromarginata,* and *nigrimontis* groups reflect true relationships, but the *stenogon* and *translineata* groups include more diverse forms and may represent more than one phylogenetic line. Two species with unique specializations, *bidens* and *tuberosa,* are placed in groups by themselves; their affinities are obscure. This species group arrangement,

therefore, is somewhat artificial, and the groups are best considered ones of convenience, chosen for clarity of presentation, rather than natural representations of lines of evolution.

This paper, then, presents a modern diagnosis of *Sigmoria,* with descriptions and redescriptions of all species and subspecies, and discussions of their ecologies, ranges, and phylogenies. All pertinent holotypes were examined except that of *Deltotaria nigrimontis,* for which paratypes are available. The holotype of this species is not in the American Museum of Natural History as reported by Chamberlin (1947) and Chamberlin and Hoffman (1958), and its current location is unknown. Unless otherwise indicated in species accounts collections were made by the author and assistants. The acronyms PNF and CNF are used throughout the text to denote the Pisgah National Forest of North Carolina and the Cherokee National Forest of Tennessee, respectively, and GSMNP signifies the Great Smokey Mountains National Park. Acronyms of sources of preserved study material cited in the text are as follows:

AMNH — American Museum of Natural History, New York, NY.
ANSP — Academy of Natural Sciences, Philadelphia, PA.
FSCA — Florida State Collection of Arthropods, Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Gainesville, FL.
JAB — Private collection of Joseph A. Beatty, Carbondale, IL.
MNHP — Museum National d'Histoire Naturelle, Paris, France.
NCSM — North Carolina State Museum of Natural History, Raleigh, NC.
NMNH — National Museum of Natural History, Smithsonian Institution, Washington, DC.
RLH — Private collection of Richard L. Hoffman, Radford, VA.
RVC — Private collection of the late Ralph V. Chamberlin, now being accessioned by the NMNH.
WAS — Private collection of William A. Shear, Hampden-Sydney, VA.

Literature Review

Of the genera considered here, *Sigmoria* contains the most species, has received the most attention in the past, and is in the greatest state of confusion. It was erected by Chamberlin (1939) for "large, robust species which are characterized by the sigmoidally curved blade of the telopodite." *Sigmoria munda* was designated type species, *Fontaria evides* was transferred into the genus, and four additional species were described: *aberrans,*

conclusa, divergens, and *mariona.* In the ensuing years Chamberlin added *brachygon* (1940a), *stenogon* (1942), *houstoni* (1943), *gracilipes* (1947), and *zyga* (1949) to *Sigmoria.* Hoffman proposed *Sigmoria furcifera* (1949), transferred *Fontaria latior* and *mimetica* into the genus (1950a), and described *nigrescens* (1950b). Hoffman (1950a) also summarized the 15 species in *Sigmoria* at that time and provided short synonymies, type localities, repositories of type specimens, and distributional information. His generic diagnosis, while longer than Chamberlin's, still did not provide the critical characters needed to identify the genus with certainty. The North American checklist by Chamberlin and Hoffman (1958) included a similar summary in shortened form. Hoffman (1959) proposed *nantahalae* and, noting that it had become a "catch-all" for xystodesmids not readily conforming to other genera, suggested that *Sigmoria* could include forms with a triangular process on the inner edge of the telopodite about a third of the way back from the distal end. This statement by Hoffman represents the only previous progress toward characterization of *Sigmoria.*

Since 1958 the composition of *Sigmoria* has been substantially reduced through synonymy or transfer of species to other genera. The first such action was the return of *evides* to *Fontaria* by Keeton (1965). The identity of this species had never been established, and he concluded that, although it might belong in *Brachoria,* the best course was to retain *F. evides* as a *nomen inquirendum.* Hoffman (1967) transferred *divergens* and *nigrescens* to *Cleptoria,* reducing the latter to a subspecies of the former. Shelley (1976) reduced *mariona* to a subspecies of *latior,* and synonymized *aberrans, conclusa,* and *furcifera* with *latior latior.* This action was followed by the transferral of *gracilipes* to *Brachoria* (Shelley 1979a), leaving *Sigmoria* with the established species and subspecies listed chronologically below with their type localities. The only other mention of *Sigmoria* was by Hoffman (1979), who considered *Sigiria* a synonym and estimated that *Sigmoria* contained about 18 species in the southern Appalachian region.

Sigmoria latior latior (Brolemann, 1900). Restricted to south of the Deep Cape Fear Rivers, NC, by Shelley (1976).

l. mariona Chamberlin, 1939, Marion, McDowell Co., NC.

l. hoffmani Shelley, 1976. 4.4 miles NW North, Orangeburg Co., SC.

S. mimetica (Chamberlin, 1918). Near Nashville, Davidson Co., TN.

S. munda Chamberlin, 1939. Hot Springs, Madison Co., NC. TYPE SPECIES.

S. brachygon Chamberlin, 1940a. Glen Bald, Bent Creek Forest Experiment Station, PNF, Buncombe Co., NC.

S. stenogon Chamberlin, 1942. Bennett Gap Road, PNF, Transylvania Co., NC.

S. houstoni Chamberlin, 1943. Said to be Houston, Harris Co., TX, but probably collected somewhere in Franklin, Grundy, or Marion Cos., TN, the only places where it has been authentically taken.

S. zyga Chamberlin, 1949. Near Hot Springs, Madison Co., NC.

S. nantahalae Hoffman, 1958. Natahala Gorge, Swain Co., NC.

Immediately after erecting *Sigmoria,* Chamberlin (1939) proposed *Sigiria* as "suggesting *Brachoria,* but the blade of the telopodite not segmented and the subapical portion broadly expanded." As with *Sigmoria,* the diagnosis of this new genus was but a single sentence, and in this case based on what the genus suggested rather than a description of the form itself. The type species, by original designation, was *Sigiria scorpio* Chamberlin, but Hoffman (1950b) transferred *Fontaria rubromarginata* Bollman into *Sigiria,* listing *scorpio* as a junior synonym. Chamberlin and Hoffman (1958) brought *Deltotaria nigrimontis* Chamberlin and *Apheloria intermedia* Hoffman into the genus, and Hoffman (1979) placed *Sigiria* in synonymy under *Sigmoria,* an action I now believe to be correct. The composition of *Sigiria* before this action was as follows:

Sigiria rubromarginata (Bollman, 1887). Balsam, Jackson Co., NC.

S. nigrimontis (Chamberlin, 1947). "Black Mountain," NC. Chamberlin and Hoffman (1958) cited the type locality as the town of Black Mountain in Buncombe County. However, the species has never been collected in or near this community, and the locality apparently is an unknown section of the Black Mountain range, located in the contiguous corners of Buncombe, Yancey, and McDowell counties. The North Carolina Gazetteer (Powell 1968) does not mention a peak by this name in the range, and thus the type locality cannot be stated more specifically than just the Black Mountains of North Carolina.

S. intermedia (Hoffman, 1948a). Asheville, Buncombe Co., NC.

The nominal genus *Falloria* is monotypic and was erected by Hoffman (1948b) for *Apheloria bidens* Causey. It was included in the North American checklist by Chamberlin and Hoffman (1958) and listed by Hoffman (1979), who stated that it included one species in Tennessee. *Falloria* is here placed in synonymy under *Sigmoria.*

Taxonomic Characters

The taxonomically important characters of *Sigmoria* involve chiefly the male gonopods. Color patterns and aspects of the pregonopodal sterna of males are of limited value in identifying species and in distinguishing the genus from sympatric apheloriine taxa. In the eastern Piedmont and

Coastal Plain of North Carolina, which have limited xystodesmid faunas, color, body proportions, presence or absence of coxal tubercles on the walking legs, and shape of the midbody sterna are reasonably reliable criteria for determining genera of females and late instar juveniles. However, the complexity of the apheloriine faunas in the Blue Ridge Mountains, eastern foothills, piedmont South Carolina, Ridge and Valley Province, and Cumberland Plateau makes the collection of males in these regions mandatory for positive generic determinations. The only somatic features which authentically determine species of *Sigmoria* are the color patterns of *nantahalae* (red paranota, white metatergal stripes) and *leucostriata* (white or light yellow paranota and concolorous stripes) and the densely hirsute postgonopodal sterna of *tuberosa*. Otherwise, the only sure way to make specific identifications is by examining the male genitalia. New gonopodal terminology, devised to identify sections of the acropodite, is explained in the gonopod paragraphs and illustrated in figures 3, 4, 97, and 98.

Coloration.— Several colors and color patterns are evident among the species and subspecies of *Sigmoria,* and these too are useful clues to the identity of an individual of either sex. All forms display black metaterga and colored paranota, and there may or may not be transverse connecting stripes along the caudal edges of the metaterga and the anterior edge of the collum. The width of these stripes varies from a narrow line, as on the anteriormost segments of *sigirioides,* to broad bands nearly half the width of the metaterga on large species such as *lyrea*. The color of the stripes is a very important feature, however, and in individuals with orange, yellow, white, violet, or purple paranota, the metatergal stripe, if present, is essentially concolorous with the paranota. However, in striped species with red paranota, the band may be either red, white, or blue. *Sigmoria stenoloba* and *latior latior* have red, orange, or yellow paranota but lack stripes. Table 1 summarizes the typical color and color patterns for each species and subspecies of *Sigmoria,* omitting occasional variations exhibited by certain species, particularly by *bidens* and *translineata*. Taxa which typically are polymorphic for color and/or pattern are indicated by an asterisk. Although paranotal spots of northern individuals of *stenoloba* are indented toward the midline along the caudal edge of the metaterga, thus resembling a stripe, the markings do not actually meet to form one.

Table 1. Colors and color patterns of species and subspecies of *Sigmoria*.

Pattern	Color	Taxa
Paranotal spots only	red, orange, or yellow	*stenoloba, latior latior,* some *latior* intergrades*
Paranotal spots & metatergal stripes	both yellow to orange	*simplex**, *areolata, latior munda**, some *latior* intergrades*
"	both red	*simplex**, *truncata, sigirioides, quadrata, laticurvosa, stibarophalla, latior munda**, *l. hoffmani,* some *latior* intergrades*, *rubromarginata, triangulata, nigrimontis*
"	both violet or purple	*stenogon, disjuncta*
"	both white or light yellow	*leucostriata*
"	paranota red, stripes blue	*fumimontis, bidens, translineata, lyrea, tuberosa, xerophylla*
"	paranota red, stripes white	*nantahalae*

Sterna.— The only aspects of the sterna that aid in identifications are the configuration and degree of development of the process(es) of the 4th sternum, and to a lesser extent those of the 5th. *Sigmoria tuberosa* can be identified by the denser pilosity on the caudal edges of the postgonopodal sterna in males and midbody sterna in females, but aside from this specific trait of *tuberosa,* postgonopodal sternal differences have no taxonomic utility.

The process of the 4th sternum is highly variable, ranging from two separate lobes that are much shorter than the width of the adjacent coxae, as in *latior,* to a single spine that is longer than the adjacent podomeres, as in *tuberosa.* In general, species of the *latior* group have very short projections that are more deeply divided than in other groups. The process is also short and deeply divided in the *leucostriata, simplex,* and *stenogon* groups, but it is subequal to the width of the adjacent coxae in the *quadrata* and *translineata* groups. Table 2 summarizes the length of the 4th sternal process relative to the widths of the adjacent coxae.

The processes of the 5th sternum are always smaller than that of the 4th and consist of two rounded knobs between the anterior (4th) legs, and elevated flattened areas between the posterior (5th). The knobs are usually shorter, never longer, than the width of the adjacent coxae, and the elevated, flattened areas are usually rather indistinct. Only in *fumimontis* and *tuberosa* are the anterior knobs as long as the coxae, and it is in these two species that the posterior projections reach their maximum develop-

Table 2. Length of process of 4th sterna of species of *Sigmoria*.

Shorter (than widths of adjacent coxae)	Subequal	Longer
latior	*quadrata*	*tuberosa*
stenoloba	*laticurvosa*	
areolata	*translineata*	
stibarophalla	*lyrea*	
simplex	*fumimontis*	
truncata	*bidens*	
sigirioides		
stenogon		
nantahalae		
leucostriata		
xerophylla		
rubromarginata		
triangulata		
nigrimontis		
disjuncta		

ment, becoming knobs nearly as long as the anterior ones. In *lyrea, quadrata,* and *laticurvosa* the anterior processes are coalesced medially into a single structure that is located in the midline; however, the caudal elevations are indistinct in these three species.

Gonopodal characters.— 1. *Terminology.* The acropodite[2] of the gonopod extends in a ventral or ventromedial direction from the prefemur and protrudes from the aperture. At about 1/3 of the total acropodite length it bends in an anterior direction, and at 2/3 to 3/4 of its length it curves dorsally or dorsolaterally toward the body. This general curvature forms an arch in medial or lateral view, and since some of the specific differences involve modifications of the generalized curvature, new terminology is needed to distinguish the sections of the acropodite from each other. Various laminate flanges and other projections extend from some of these sections. The gonopods of *latior latior,* in figures 1-2, and *rubromarginata rubromarginata,* in figures 97-98, are labeled with the complete terminology for all sections of the acropodite and its processes.

[2]The term "telopodite" refers to all parts of the gonopod distal to the coxa. Since in polydesmoids gonopods consist of only two segments, the word therefore refers to only the one outer segment. The term "acropodite" refers to the glabrous, groove-carrying part of the telopodite distal to the prefemur; hence in xystodesmids, telopodite = acropodite + prefemur. In the ensuing species accounts I have endeavored to use telopodite only when referring to the entire distal segment, including the prefemur, and acropodite when referring to sections distal to the prefemur.

The basal portion of the acropodite arising from the prefemur is the "basal zone." It ends at the "anterior bend," which leads into a long section forming the "peak" of the arch. The peak ends at the beginning of the "apical curve," and the portion of the acropodite forming the apical curve is the "distal zone." The ending of the distal zone and the acropodite is the "tip." In all species except *nantahalae,* there is a laminate "medial flange" in one of two locations on the medial face of the acropodite, either the proximal portion of the peak or the proximal portion of the distal zone. In some species the medial flange is vestigial. In addition to the medial flange, some species also possess a triangular subconical, or subrectangular "tooth" on the medial face of the peak distal to the flange or lobe of the flange. Laterally, some species exhibit a "lateral flange" on the distal zone, which usually begins at either the apical curve or on the distal extremity of the peak. In *triangulata,* however, the lateral flange is entirely on the peak. The tooth and lateral flange are the most common adornments of *Sigmoria,* but additional lamellae, lobes, or other projections occur in certain species. A discussion of each section of the acropodite and its taxonomic utility is presented after descriptions of the *in situ* arrangements, prefemoral process, and thickness of the acropodite.

2. *In situ arrangements.* The *in situ* arrangement of acropodites in the aperture helps to distinguish *Sigmoria* from sympatric apheloriine genera. Two arrangements are most common. One, demonstrated by *latior* (Fig. 2), has the peaks of the two acropodites overlapping in the midline of the aperture and curving over the opposite side of the opening. In the apical curve regions, the acropodites usually curve back toward or across the midline, and the tips of the structures also overlap. In some cases the tips are actually hooked together so that the acropodites form a single interlocking unit. The distal zones often curve forward beyond the anterior margin of the aperture, and the sternum between the 7th legs is convexly recessed, to accommodate the apical curvatures when the body segments are compressed. The degree to which the peaks curve over the opposite side of the aperture varies with the species. It is greatest in *stenogon* and *tuberosa,* whose acropodites curve so strongly that they lie almost entirely over the aperture. This *in situ* arrangement, hereafter termed "overlapping," is visible to the naked eye and aids in field identifications.

The second common pattern is termed "crossing," and is demonstrated primarily by species formerly in *Sigiria* (Fig. 96). In this arrangement the acropodites extend in a ventromedial direction from the prefemora and protrude from the aperture. They curve broadly anteriomediad and cross over or under the opposite acropodite in the midline of the aperture. The point of crossing is usually from midlength of the peak to the beginning of the

apical curve. Just distal to the point of crossing the two acropodites curve sharply or broadly dorsad, and the arcs of the apical curves extend slightly beyond the anterior margin of the aperture. As with the overlapping arrangement, when the body segments are compressed, the apical curvatures fit between the posterior (7th) legs of the 6th segment, and the sternum between these legs is slightly recessed to accommodate these structures.

Thus, the overlapping and crossing arrangements differ in the number of places the acropodites cross — two in the former, one in the latter — and the degree to which they overlie the opposite side of the aperture. In the crossing pattern the acropodites extend more directly anteriad with only minimal overlying of the opposite side of the aperture and do not project as directly anteriad.

A few species depart from either of these patterns, and this is generated by structural peculiarities in *stibarophalla.* In this species the acropodite and medial flange are so massive that there is steric hindrance and insufficient space for the gonopods to assume an overlapping arrangement. Consequently, one acropodite lies across the opposite side of the aperture in typical overlapping fashion, and the other extends almost directly anteriad over the 6th sternum (Fig. 24). An entirely different pattern, termed "parallel," is displayed by *translineata* and some individuals of *simplex* (Fig. 67). Here the acropodites do not cross the midline of the aperture but lie beside each other and extend forward in parallel fashion over the anterior margin of the opening and the 6th sternum. The distal zones either curve dorsad in the same pattern or diverge dorsolaterad. The peaks may or may not touch in the midline, but they do not overlap. Few other apheloriine taxa demonstrate the parallel pattern, but it is common in the Rhysodesmini and displayed by the genera *Pleuroloma* and *Cherokia.*

3. *Prefemoral Process.*— The prefemoral process in *Sigmoria* is highly variable and an effective specific criterion for only *bidens, translineata,* and *lyrea.* In *bidens,* the process is greatly enlarged with a subglobose base, and extends beyond the level of the tip of the acropodite; in *translineata* and *lyrea,* it is divided basally into two long subequal components which are reduced in *fumimontis,* the other species in that group. The structure is short and wedge-shaped in most of the other species and may or may not be apically bifurcate. *Sigmoria areolata, stenogon,* some forms of *latior,* and species of the *quadrata* group possess a longer process that is bent ventrad at some point, usually near midlength.

4. *Characters of the acropodite. a) Thickness.*— The thickness of the acropodite varies greatly in *Sigmoria* and is an important characteristic of some species apart from the actual configuration of the structure. In *stenogon* and *sigirioides* the acropodite is particularly thin and fragile,

easily broken during dissection. The opposite situation occurs in *fumimontis* and *stibarophalla,* which have heavy, massive gonopods. The remaining species fall between these extremes, some closer to one than to the other.

b) General curvature.— In many species of *Sigmoria* the stem of the acropodite passes through several vertical planes in the total curvature. The standard two dimensional medial drawing is therefore misleading in portraying the structure as uniplanar when the peak is actually above the plane of the paper and on a different level from the basal and distal zones. The latter are coplanar for much of their lengths, particularly the parts farthest from the peak. There is considerable variation in this pattern, however, as species of the *simplex* and *leucostriata* groups are nearly uniplanar, and in species formerly in *Sigiria,* the acropodite is essentially coplanar throughout its length.

In many species of *Sigmoria* the acropodite, as seen in medial view, roughly resembles the number 7. That is, the peak is long and flattened, and the arch overhangs and extends well beyond the level of the prefemoral process. This pattern is shown most clearly by the *latior* group, and is illustrated in Figure 3. In *sigirioides* and the *quadrata* group, however, the peak is shorter and the distal zone is almost directly above the prefemoral process, so that an enclosed circular or rectangular unit is suggested. In the *rubromarginata* group the anterior bend and apical curve are broad, poorly defined, and continuous through the peak; and the acropodite forms a smooth, continuous curve. The distal zone tends to be long and curves downward from the peak, and the overall appearance of the gonopod resembles a question mark (?). For most species of *Sigmoria* a profile of the acropodite is visible in medial or laterial view, but in *fumimontis* and *translineata,* the peaks are tilted mediad so that the lateral edge is noticeable in medial view. A lateral view of these two species thus reveals more of the undersurface of the medial flange than is seen in the other species.

c) Basal zone.— The basal zone has less taxonomic significance than other sections of the acropodite. It is usually about 1/3 of the total length of the acropodite, but is proportionately much longer in *truncata* due to the absence of the distal zone. The tubercles in *tuberosa* are located on the basal zone as are the basal lobes of *latior, stenoloba, quadrata,* and *stibarophalla.*

d) Anterior bend.— The anterior bend marks the end of the basal zone and the beginning of the peak. In species like *latior,* where the bend is sharp and distinct (approximately 90°), it is said to be "well defined." However, in species like *laticurvosa* the anterior bend is broad, and the exact location is obscure. In these species the bend is described as "poorly defined."

e) Peak. — The peak is the portion of the acropodite arch between the anterior bend and apical curve. It is usually long (1/3 or more of the

acropodite length) and flattened, but is gently curved in some species, most notably those of the *simplex* and *rubromarginata* groups. The peak is part of the continuous curve of the acropodite in *laticurvosa* and *lyrea*. Although flattened, the peak rises in *fumimontis* so that the apex is at the distal extremity beside the apical curve. The most unusual modification of the peak is shown by *areolata,* in which it is flexed ventrad at midlength. In some species the medial flange projects from the proximal portion of the peak, and the tooth, when present, is usually located just distal to the flange. In *nigrimontis angulosa* and *disjuncta* there is an additional flange on the inner surface of the peak, and *triangulata* is unique in having the lateral flange entirely on this section.

f) Apical curve and distal zone.— The apical curve is the arc distal to the peak formed by the distal zone of the acropodite. It usually has a broad diameter, as the distal zone curves back beneath the peak (as seen in medial view) and is directed toward the basal zone. In *stibarophalla,* however, the curve is very narrow, and the distal zone is tucked tightly under the distal extremity of the peak. In *sigirioides* and *quadrata* the curve is essentially a right angle bend, as the distal zone is nearly perpendicular to the peak. In species such as *latior,* where the beginning of the apical curve is obvious, it is said to be "well defined," but in species like *lyrea,* where the curve is broad with no clear beginning, it is described as "poorly defined." The length of the distal zone varies greatly, being longest in *lyrea,* where it extends to the level of the base of the prefemoral process, and shortest in *stibarophalla, areolata, nigrimontis nigrimontis,* and *disjuncta.* It is absent completely from *truncata.* In *tuberosa* the distal zone possesses a flange on the inner surface for about half its length, diagnostic for the species.

g. Tip.— In most species of the *latior* group, the distal zone terminates in a lamina on the medial edge which is reflected at a sharp angle from the blade of the zone and directed into the arch (Fig. 2). Such a termination is said to be "reflexed," and the prostatic groove opens at its extremity. In the *simplex, quadrata, rubromarginata,* and *nigrimontis* groups the termination is the unmodified end of the distal zone without a separate lamina, and this tip is labeled "simple" or "not reflexed." A non-reflexed tip may or may not be angled sharply from the distal zone, but the key point is whether or not a separate lamina is involved, and this is best seen in medial view. The tip of *lyrea,* and to a lesser extent those of *leucostriata* and *xerophylla,* are shaped like the reflexed tip of *latior* and directed at about the same angle into the arch; however, it is a smooth continuation of the distal zone and not a separate lamina. This particular tip is called "pseudoreflexed," since it appears to be reflexed but is not. The tip of *tuberosa* is complex and consists of three parts — a small reflexed lamina, a subterminal lobe, and a

blunt central part. The lamina, however, is on the lateral, rather than the medial, side and is much smaller than that of *latior;* the prostatic groove in *tuberosa* opens on the inner corner of the central part rather than on the lamina as in all species with a reflexed tip.

h) Medial flange.— Except for *nantahalae,* all species of *Sigmoria* possess a laminate flange on the medial face of the acropodite, either on the proximal portion of the peak or the proximal portion of the distal zone. In some forms, particularly in the *nigrimontis* group, the structure is vestigial. In most species with the flange on the peak, it arises at or very near the anterior bend and terminates at about 2/3 of the length of the peak, but in *stenogon* and *stibarophalla* it terminates on the distal zone. In specimens of *stibarophalla* from the eastern part of its range in Rutherford County, North Carolina, the flange continues around the beginning of the apical curve onto the lateral side of the acropodite. In species like *latior,* where the flange is broad and obscures a small section of the stem of the acropodite, it is said to be "well demarcated" from the latter. Conversely in *fumimontis,* where the flange is narrow and the distinction between it and the acropodite is not clear, the flange is said to be "poorly demarcated" from the stem.

i) Tooth.— The tooth, if present, is usually located on the medial face of the peak distal to the flange. The two exceptions are *bidens,* in which the tooth is on the distal zone, and *nantahalae,* in which it is on the peak at about 2/3 of its length, but there is no flange. The tooth is usually a thin lamella, but in these two species, it is thicker, being subconical in *bidens* and subrectangular in *nantahalae.* The distance between the tooth and distal extremity of the flange is variable; they are adjacent to each other in *latior,* but slightly separated in *stenoloba.* The two structures are fused in *tuberosa,* and in *areolata* they are separated but part of the same lamina.

j) Lateral flange.— In most species of *Sigmoria* there is an apical flange on the lateral side of the acropodite, arising on the distal extremity of the peak or the beginning of the distal zone, and terminating on the latter proximal to the tip. It ranges from long and narrow to broadly rounded, and varies greatly in *stenogon,* where it may be absent, subtriangular, or long and subrectangular.

k) Prostatic groove.— The prostatic groove arises in a pit near the base of the prefemur, runs along the medial face of the prefemur and distal zone, and usually crosses to the lateral side of the acropodite at the anterior bend. However, in some forms of *nigrimontis* it stays on the medial side or crosses over distally, near the apical curve. In *disjuncta* the crossing occurs on the prefemur, and the groove runs entirely on the lateral side of the acropodite. This feature is the principal diagnostic character for this species.

Genus SIGMORIA Chamberlin

Sigmoria Chamberlin, 1939:7. Hoffman, 1950a:1-2. Chamberlin and Hoffman, 1958:49. Hoffman, 1979:158.

Sigiria Chamberlin, 1939:9. Chamberlin and Hoffman, 1958:48.

Falloria Hoffman, 1948b:93-94. Chamberlin and Hoffman, 1958:33. Hoffman, 1979:159. **NEW SYNONYMY.**

Type species.— Of *Sigmoria, S. munda* Chamberlin, 1939, by original designation; of *Sigiria, S. scorpio* Chamberlin, 1939, by original designation; of *Falloria, Apheloria bidens* Causey, by original designation.

Description.— A genus of small to large xystodesmids with the following characteristics:

Body composed of head and 20 segments in both sexes; size varying from large, robust forms of 10+ mm wide and 42-50+ mm long, to small, delicate individuals of less than 7.5 mm wide and under 35 mm long; W/L ratio similarly varying from about 20-28%. Body essentially parallel sided in midbody region, tapering at both ends.

Color in life variable; most forms with black base color, reddish paranota, and concolorous red or bluish transverse stripes along caudal margins of metaterga and anterior margin of collum connecting paranotal markings, width of stripes variable; some forms with red paranota and white stripes, yellow paranota and yellow stripes, and white paranota and white stripes; others with red, orange, or yellow paranota but without metatergal stripes.

Head of normal appearance, usually smooth and polished, occasionally finely granulate. Epicranial suture distinct, terminating in interantennal region, not apically bifid; interantennal isthmus variable; genae not margined laterally, with shallow central impressions, ends broadly rounded and projecting slightly beyond adjacent cranial margins. Antennae moderately slender, varying in length, becoming progressively more hirsute distally, with 4 conical sensory cones on ultimate article; no other sensory structures apparent. Facial setae reduced; epicranial and interantennal absent, clypeal and labral present, with or without frontal and/or genal setae.

Terga usually smooth and polished, occasionally finely granulate, becoming coriaceous in paranotal regions. Collum variable, ends subequal to or extending well beyond those of following tergite. Paranota mildly to strongly depressed; caudolateral corners rounded on anteriormost segments to various midbody segments, becoming blunt and progressively more acute posteriorly. Peritremata distinct but relatively flat, not strongly elevated above paranotal surface; ozopores usually located just caudal to midlength, opening dorsad to dorsolaterad. Prozonites smaller than metazonites; strictures moderately distinct, slightly costulate.

Caudal segments normal for family.

Sides of metazonites irregular, with varying shallow, curved impressions. Pregonopodal sterna of males variously modified; that of segment 4 with medial process of variable length, shorter, subequal, or longer than width of adjacent coxae; sternum of segment 5 with two knob-like processes of varying lengths between 4th legs, coalesced into single medial process in some forms, with variable elevated flattened areas or ridges between 5th legs; sternum of segment 6 convexly recessed to varying degrees, sometimes deeply excavated, between 7th legs to accommodate apical curvatures or acropodites when body segments compressed; 7th legs occasionally set slightly farther apart than 6th. Postgonopodal sterna mostly glabrous but variable in configuration; with or without small, blunt lobes subtending both pairs of coxae, and with or without various shallow grooves and impressions, in particular narrow, transverse grooves between leg pairs, and wide, central impressions. Gonopores on second pair of legs of males short to elongate, with round, apical knobs. Coxae usually with varying distomedial projections beginning on midbody (postgonopodal) legs, ranging from low blunt tubercles to apically

acute spines; prefemoral spines relatively long and sharply pointed; tarsal claws bisinuate. Hypoproct broadly rounded; paraprocts with margins strongly thickened.

Gonopodal aperture broadly ovoid to elliptical, usually indented and slightly narrower anteriolaterally, sides elevated above metazonal surface. Gonopods *in situ* with variable configurations; usually with each acropodite extending mediad beyond midline of aperture and over- or under-lapping other acropodite proximal to midlength in midline, curving slightly anteriolaterad over opposite side of aperture then back over midline with tips curving dorsad and crossing, apical curvatures extending to varying lengths over anterior margin of aperture and sternum of segment 6; some species with acropodites crossing only once in peak or apical curve regions in midline of aperture, apical curves extending anteriad only slightly beyond anterior margin of aperture; others with acropodites not overlapping but medial edges touching or nearly touching in midline and extending anteriad in subparallel arrangement over anterior margin of aperture and sternum of segment 6, apical portions or curvatures in these forms projecting either dorsad or dorsolaterad. Coxa moderate to large, without apophysis, connected by membrane only, no sternal remnant. Prefemur moderate in size, usually with highly variable prefemoral process arising on anteriomedial side. Acropodite thin and fragile to thick and massive, curved through one or more vertical planes in vaguely sigmoidal configuration as follows: basal zone extending subventrad from prefemur; bent sharply or broadly anteriad (anterior bend) at no more than 1/3 of total length of structure; curved sharply or broadly subdorsad apically (apical curve) near 2/3-3/4 length, usually forming arc with variable diameter; portion between anterior bend and apical curve (peak of arch) bowed mediad and not coplanar with basal and distal zones or coplanar with latter regions, flattened or high and gently rounded in medial view, extending to or beyond level of prefemoral process; region forming apical curve (distal zone) varying in length, either projecting directly dorsad or curved inward into arch of acropodite, usually essentially coplanar with basal zone, either of subequal width throughout most of length (except extreme tip) or tapering smoothly to acuminate tip. Termination variable; either blunt or acuminate unmodified end of distal zone or small, reflexed lamina on medial edge directed at sharp angle (often perpendicularly) from distal zone; termination occasionally angled from distal zone but not separated into distinct lamina. Peak of arch with or without flange of variable length, width, and configuration on medial edge, arising at or near anterior bend, terminating from near midlength of peak to proximal portion of distal zone; with or without variable subtriangular laminate tooth arising from medial edge distal to flange, separated to varying lengths from flange, occasionally fused to flange. Distal zone with or without variable flanges or lobes proximally on both medial and lateral sides, one or both often arising on distal extremity of peak, medial flange much smaller than lateral, vestigial on some forms; also with or without long, narrow, laminate flange on lateral side, arising near beginning of apical curve, terminating proximal to tip, flange occasionally modified into subtriangular lobe or long, narrow, subrectangular projection. Acropodite occasionally with additional flange, lobe, or tubercles at various positions. Prostatic groove arising in pit on prefemur, running along stem of acropodite and opening terminally on tip of distal zone or on reflexed lamina when present.

Cyphopodal aperture short and very broad, encircling 2nd legs, sides either flush with or elevated above metazonal surface. Cyphopods *in situ* located lateral to 2nd legs, side of receptacle usually visible in aperture with valves directed caudad or caudolaterad, oriented subdorsoventrally in body; occasionally with valves visible in aperture; receptacle located dorsomediad adjacent to coxae. Receptacle variable, either large and cupped around ventral end of valves or small and separated from valves; surface either finely granulate or convoluted with folds and ridges. Valves small to moderate and subequal in size, surface usually finely granulate, occasionally with ridges. Operculum minute, located under free end of valves.

Synonymy.— Retention of the names *Sigiria* and *Falloria* can no longer be justified. The gonopods of the species formerly in *Sigiria* exhibit features which grade into those possessed by the type of *Sigmoria. Sigmoria leucostriata* demonstrates characters of both taxa thus justifying their combination. By the rules of nomenclature *Sigmoria* has priority since Chamberlin proposed it two pages ahead of *Sigiria* in the same paper. The gonopods of the species for which *Falloria* was proposed, *Apheloria bidens,* display the basic characters of *Sigmoria munda,* including the *in situ* arrangement in the aperture, the acropodite curvature, and the medial flange on the proximal portion of the peak. Thus, *bidens* is readily accommodated by *Sigmoria,* which has nine years priority over *Falloria.*

Range.— Parts of the Appalachian Plateau, Ridge and Valley, Blue Ridge, Piedmont Plateau, and Coastal Plain Physiographic Provinces of the eastern United States, ranging south from southern West Virginia to the mountains and foothills of north Georgia and the Coastal Plain of southern South Carolina, west to the Blue Ridge Province of eastern Tennessee and east to the Coastal Plain of southeastern North Carolina (Fig. 131). The genus occupies an irregular range within this area; for example, the Appalachian Plateau and Ridge and Valley Provinces are inhabited only in southern West Virginia and southwestern Virginia; farther south, at the latitude of the Great Smoky Mountains in Tennessee, the westward limit is the western periphery of the Blue Ridge Province. The Savannah River is the southern boundary in South Carolina, but in the mountains west of the eastern continental divide, *nantahalae* and *xerophylla* extend into the southern section of the Blue Ridge Province in north Georgia, and *disjuncta* occurs in the piedmont foothills of that state (Fig. 138). In the north, *latior* occurs in southern West Virginia in the mountains, but in the Piedmont Plateau it does not range beyond the Neuse River basin of central North Carolina and is thus absent from piedmont Virginia. The easternmost records of *Sigmoria,* also of *latior,* are from Brunswick County, North Carolina, and Charleston-Colleton counties, South Carolina, where it occurs in Edisto Beach State Park within a few meters of the Atlantic Ocean (Fig. 139).

Species.— Twenty-two are known, three of which are divided into a total of nine subspecies. Three species — *mariona, brachygon,* and *zyga* — are herein synonymized with *latior munda (mariona* and *brachygon)* and *rubromarginata rubromarginata (zyga).* Two species — *mimetica* and *houstoni* — are transferred out of *Sigmoria* but left unassigned. They will be discussed in future papers. Additional species of *Sigmoria* may remain to be discovered, particularly in remote inaccessible areas of the southern Blue Ridge Province.

Key to Species of Sigmoria
(based primarily on adult males)

Devising a key that will distinguish the 22 diverse species of *Sigmoria* is a most difficult task. Few comments can be made about any one species that would not also apply to another, and the total range of variation in most species is such that very little can be said that will not exclude an important variant. *Sigmoria latior,* for example, is such a variable species that it cannot be effectively treated in a key to species. Many remarks about one form of *latior* would tend to exclude another, and subspecies are therefore used in the key. However, *rubromarginata* and *nigrimontis,* the other two species which are divided into races, are treated as species in the key, and all subspecies and intergrades key out at the same couplet. Except for the lateral flanges, all characters used in the following key are best seen in medial view, particularly those comparing two structures, such as ". . . extending to near level of prefemoral process." Appropriate figure numbers, along with generalized range descriptions, are thus provided to enhance the utility of the key.

1. Gonopods with variable medial flange, occasionally vestigial, either on proximal portion of peak or on distal zone 2
   Without this character (Fig. 63); Swain Co., NC, to Towns and Union cos., GA ..... *nantahalae* Hoffman
2. Medial flange on proximal portion of peak (Figs. 3, 31, 45, 57, 68, 81, 84, 92) 3
   Medial flange on distal zone (Figs. 97, 105, 108, 114, 129) 20
3. Medial flange small, not obscuring stem of acropodite in medial view; distal zone with opposing proximal lobes on medial and lateral margins, lateral lobe larger (Figs. 84, 88) 4
   Medial flange larger, obscuring at least small section of stem of acropodite in medial view; distal zone either without lobes or with lobe only on lateral side 5
4. Paranota and metatergal stripes white to light yellow; portion of distal zone distal to lobes relatively long, bent sharply into arch; lateral flange present (Figs. 84-85); Cocke and Sevier cos., TN ..... *leucostriata,* new species
   Paranota red, metatergal stripes blue; portion of distal zone distal to lobes relatively short, only slightly curved into arch; lateral flange absent (Figs. 88-89); McMinn Co., TN, to Gilmer Co., GA ..... *xerophylla,* new species
5. Acropodite with distinct tooth on peak or distal zone distal to flange (Figs. 3, 12, 21, 80, 92) 6
   Without this character 10
6. Prefemoral process greatly enlarged, subglobose basally, extending in medial view to or beyond level of tip of acropodite (Fig. 80); GSMNP, Sevier Co., TN ..... *bidens* (Causey)
   Prefemoral process variable but never enlarged or globose basally, terminating well below level of tip of acropodite 7

7. Peak flexed ventrad at midlength; distal zone projecting only short distance into arch, terminating well above level of prefemoral process; tip simple (Fig. 21); Buncombe Co., NC ..... *areolata,* new species

Peak relatively flat; distal zone longer, projecting well into arch; tip at least partly reflexed 8

8. Basal zone with tubercles on outer surface; distal zone very long, extending into arch nearly to base of acropodite and just above level of prefemoral process, with wide lamina on inner surface; tip complex, with subterminal lobe on medial edge, lateral edge reflexed (Fig. 92); Swain Co., NC ..... *tuberosa,* new species

Basal zone without tubercles; distal zone variable, but never extending to near base of acropodite, without lamina on inner surface; tip without subterminal lobe, medial edge reflexed 9

9. Medial flange narrow, poorly demarcated from stem of acropodite, depth much less than that of apical curvature; tooth usually well separated from medial flange, often greatly reduced and rounded (Fig. 12); Wilkes and Catawba cos., NC ..... *stenoloba,* new species

Medial flange broad to large, well demarcated from stem of acropodite; depth equal to or greater than that of apical curvature; tooth located at distal extremity of flange, usually subacuminate (Figs. 3, 9); southern WV to southern SC ..... *latior latior* (Brolemann), *l. hoffmani* Shelley, and *latior* intergrades

10. Prefemoral process divided basally into two long, subequal components; acropodite with lobe on lateral side near beginning of apical curve, visible in medial view (Figs. 68, 72); GSMNP, Blount Co., TN to Swain Co., NC 11

Prefemoral process simple or divided apically into two short, variable components; acropodite without lobe on lateral margin; range otherwise 12

11. Acropodite relatively thick and heavy distal to anterior bend; distal zone relatively short, terminating well above level of prefemoral process; tip simple (Fig. 68) ..... *translineata,* new species

Acropodite relatively thin and narrow distal to anterior bend; distal zone relatively long; terminating at level of division of prefemoral process near medial component; tip pseudoreflexed (Fig. 72) ..... *lyrea,* new species

12. Acropodite without apical curve; distal zone greatly reduced, terminating bluntly at distal extremity of medial flange (Fig. 37); Mitchell and Yancey cos., NC ..... *truncata,* new species

Apical curve present; distal zone variable in length but extending well beyond medial flange 13

13. Apical curve very sharp, forming arc with very narrow diameter; distal zone short, tucked under peak of arch, obscured in medial view by medial flange (Figs. 25, 27); Buncombe, McDowell, and Rutherford cos., NC ..... *stibarophalla,* new species

Apical curve broader; distal zone extending below peak, visible in medial view 14

14. Apical curve bisinuate, with two inward bends into arch; lateral flange variable, absent, subtriangular, or subrectangular (Figs. 57, 59, 60); Transylvania and Henderson cos., NC ..... *stenogon* Chamberlin

Apical curve smoothly rounded and continuous, forming arc with variable diameter; lateral flange present or absent, long and narrow when present 15

15. Lateral flange absent 16

Lateral flange present 18

16. Arch of acropodite subtending a square; peak flattened, subequal in length to distal zone (Figs. 45, 47); Lexington, Saluda, and Edgefield cos., SC ..... *quadrata,* new species

Arch of acropodite otherwise; peak gently curved or rising to apex at beginning of apical curve, shorter or longer than distal zone 17

17. Peak of arch gently curved, shorter than distal zone; medial flange relatively short margin acuminate; distal zone relatively long, projecting downward from peak (Fig. 41); Yancey Co., NC ..... *sigirioides,* new species

Peak of arch with apex distally at beginning of apical curve, much longer than distal zone; medial flange relatively long and narrow, margin variable; distal zone relatively short, projecting downward from peak or curved into arch (Figs. 31, 33); Mitchell, Yancey, and McDowell cos., NC ..... *simplex,* new species

18. Medial flange short, obscuring at most only short section of stem of acropodite; peak of arch rounded, anterior bend and apical curve more or less continuous through peak, poorly defined; distal zone curved but not projecting significantly into arch; tip simple (Figs. 51, 53); Aiken Co., SC ..... *laticurvosa,* new species

Medial flange longer, obscuring long section of acropodite stem; peak flattened, anterior bend and apical curve sharp and well-defined, not continuous through peak; distal zone curved strongly into arch; tip reflexed 19

19. Acropodite thick and heavy; medial flange relatively narrow, poorly demarcated from acropodite stem, margin straight; apical curve forming arc with relatively broad diameter; prefemoral process relatively short and wide, bifurcate to subbifurcate (Fig. 76); Blount Co., TN ..... *fumimontis,* new species

Acropodite moderately thick and heavy; medial flange relatively broad, sharply demarcated from acropodite stem; margin broadly curved; apical curve forming arc with relatively narrow diameter; prefemoral process relatively long and narrow, apically bifurcate or simple (Fig. 8); Madison Co., NC, to Spartanburg Co., SC ..... *latior munda* Chamberlin

20. Distal zone tapering to acuminate tip; medial and lateral flanges large and conspicuous; peak of arch gently rounded (Figs. 97, 105) 21

Distal zone of nearly equal width throughout, except for extreme tip; tip blunt; flanges reduced, medial often vestigial; peak either curved or flattened (Figs. 108, 114, 129) 22

21. Lateral flange subtriangular, located entirely on peak; distal zone bisinuately curved apically, directed toward prefemoral process (Fig. 105); Cocke Co., TN, to Madison Co., NC ..... *triangulata,* new species

Lateral flange with margin broadly rounded, occurring from distal extremity of peak to midlength of distal zone; distal zone bent sharply inward into arch at termination of flanges, directed toward basal region of acropodite (Figs. 97, 100, 102); Cocke and Sevier cos., TN, to Burke and Cleveland cos., NC ..... *rubromarginata* (Bollman)

22. Prostatic groove crossing to lateral side on prefemur, running entirely along lateral surface of acropodite; distal zone not coplanar with basal zone, projecting sublaterad from peak (Figs. 129, 130); paranota and metatergal stripes purple-gray; Oconee Co., SC to Dawson Co., GA ..... *disjuncta,* new species

Prostatic groove either running entirely along medial; surface of acropodite or crossing to lateral side distal to anterior bend; distal zone essentially coplanar with basal zone, extending ventrad from peak (Figs. 108, 114, 116, 123, 126); paranota and metatergal stripes red; Greene and Unicoi cos., TN, and Buncombe to McDowell cos., NC ..... *nigrimontis* (Chamberlin)

The *Latior* Group

The *latior* group contains more species and occupies a much wider area than any other group. Body size, for the most part, is midway between extremes for the genus, and the process of the 4th sternum is generally short. The acropodites are moderately thick and heavy, and with the exception of *areolata,* the tip is reflexed and the lateral flange is long and narrow. The anterior bend and apical curve are sharp and well defined, and there is usually a long, flattened peak in between which is about 1/3 of the total length of the acropodite. The prefemoral process and medial flange are highly variable, and the latter is usually clearly demarcated from the stem of the acropodite. Most of the species of *Sigmoria* possessing the tooth are in the *latior* group, but the feature is not diagnostic for the group since *stibarophalla* and *latior munda* lack it. *Sigmoria latior* is widespread in five physiographic provinces of five states, but the other species occupy limited ranges in, or on the fringes of, the southern Blue Ridge Province

Sigmoria latior (Brolemann) Fig. 139

Diagnosis.— A moderate-size species of *Sigmoria* with medial flange on proximal portion of peak and with variable coloration, paranota ranging from red to yellow, metaterga with or without concolorous stripes along caudal edges; gonopods with following diagnostic characters: prefemoral process highly variable in length and configuration, bifurcate or simple; basal zone with basal lobe on ventral surface; apical curve distinct, forming arc with variable diameter; medial flange broadly rounded, moderate to large in size, arising on anterior bend, terminating near midlength of peak, depth subequal to or greater than that of apical curve; tooth present or absent, configuration variable, a separate lamina from medial flange, located adjacent to or narrowly separated from distal extremity of flange.

Remarks.— *Sigmoria latior* is the most widespread species of *Sigmoria,* ranging from southern West Virginia to the Savannah River, and from the high water mark of the Atlantic Ocean to the North Carolina-Tennessee border (Fig. 139). It is the only species to extend into West Virginia, Virginia, and the Atlantic Coastal Plain. A high degree of genetic variability is obviously needed to adapt to the diverse environmental conditions occurring in such a large range, and this is probably reflected by color variation as shown in Table 1. The species displays three of the seven color pattern combinations of the genus; only one other species, *simplex,* with two combinations, shows more than one. Intergrades display all the patterns of *latior,* which is not surprising since, due to their central location, gene flow involves all three subspecies. Intergrade forms lacking stripes along the

caudal edges of the metaterga, a characteristic of the nominate subspecies, have now been collected in Lincoln, Cleveland, and Mecklenburg counties, North Carolina, and Chester County, South Carolina (Filka and Shelley, 1980a). All the intergrades available in 1976 were striped, leading to the conclusion that only the nominate subspecies lacked this feature.

The three subspecies of *latior* were keyed, described, and discussed by Shelley (1976), but a nomenclatorial change is now necessary for the one in southwestern North Carolina, and new localities have been recorded for all forms, including intergrades. *Sigmoria latior munda* Chamberlin replaces *S. l. mariona* Chamberlin as the correct name for the race in southwestern North Carolina, which although rare, can now be reported from the French Broad River Basin west of the eastern continental divide. Consequently, in the following subspecies and intergrade accounts, a more detailed description of *latior latior* is presented than that given in my 1976 paper. Diagnoses are recorded for the other subspecies, and full synonymies, new locality records, a few miscellaneous notes, gonopodal illustrations, and an updated range map for the species (Fig. 139) are also presented. The subspecies key from my 1976 paper is repeated below so that most of the pertinent information on *latior* will be available in one publication. Some of the descriptive comments in this key may conflict with remarks in the genus key, where distinctions from other taxa necessitated different relevant comparisons.

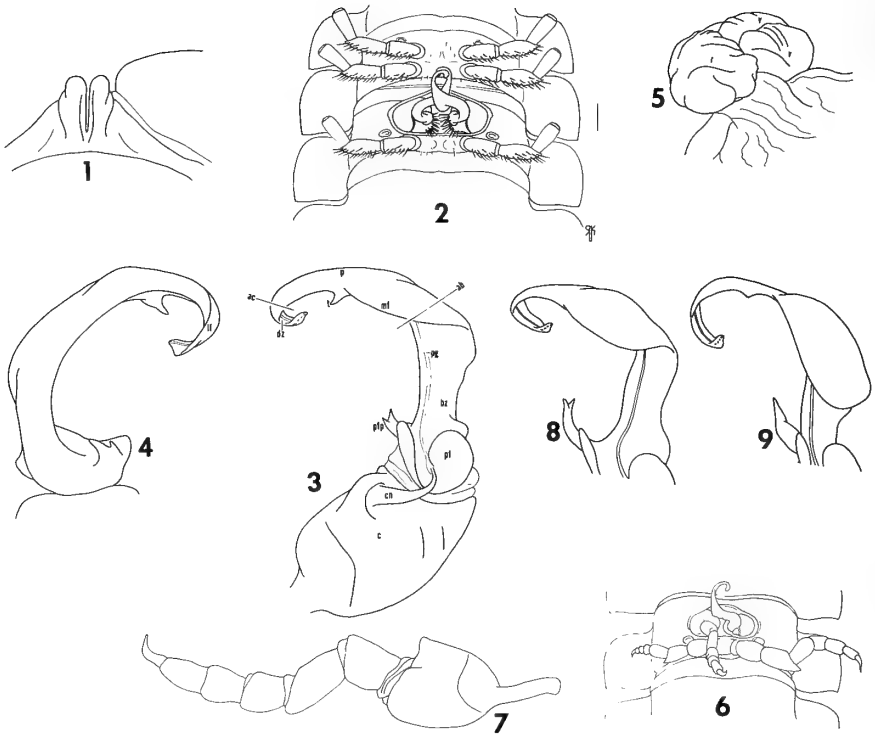
Key to Subspecies of Sigmoria latior
(based on adult males)

1. Acropodite of gonopod with tooth on medial edge distal to flange (Figs. 3, 9); metaterga with or without yellow-red stripes along caudal edges 2

   Acropodite of gonopod without tooth on medial edge distal to flange (Fig. 8); metaterga with yellow-red stripes along caudal edges; Madison Co., NC, to Spartanburg Co., SC ..... *latior munda* Chamberlin

2. Prefemoral process simple or with varying bifurcation; medial flange moderate, at maximum depth well above level of prefemoral process, subequal in depth to that of apical curvature of acropodite; apical curve of acropodite narrow, beginning closer to tip than to tooth (Fig. 3); metaterga without stripes along caudal edge; southern WV to NC north of Catawba and Deep-Cape Fear Rivers ..... *latior latior* (Brolemann)

   Prefemoral process simple, never bifurcate; medial flange greatly enlarged, extending to level of prefemoral process, depth greater than that of apical curvature; apical curve broad, usually beginning closer to tooth than to tip (Fig. 9); metaterga with red stripes along caudal edges; Piedmont and Coastal Plain of southern SC between Savannah and Congaree-Santee Rivers ..... *latior hoffmani* Shelley



FIGS. 1-9, *Sigmoria latior*. 1-7, *S. l. latior*. 1, process of 4th sternum[4] of specimen from 1.8 mi. S Moravian Falls, Wilkes Co., North Carolina, caudal view. 2, gonopods *in situ*, ventral view of specimen from same locality. 3, left gonopod of specimen from 4 mi. E Jonas Ridge, Burke Co., North Carolina, medial view. 4, telopodite of the same, lateral view. 5, left cyphopod of specimen from Linville Falls, Burke Co., North Carolina, submedial view. 6, segment 7 of abnormal male from 10 mi. SW Moravian Falls, Wilkes Co., North Carolina, ventral view. 7, right anterior appendage from this segment, medial view. 8, *S. l. munda*, telopodite of left gonopod of specimen from Marion, McDowell Co., North Carolina. 9, *S. l. hoffmani*, telopodite of left gonopod of holotype, medial view. Scale line for fig. 2 = 1.00 mm; line for other figs. = 1.00 mm for 1, 3-5, and 8-9; 0.25 mm for 6; and 0.33 mm for 7. ab, anterior bend; ac, apical curve; bz, basal zone; c, coxa; cn, cannula; dz, distal zone; lf, lateral flange, mf, medial flange; p, peak; pf, prefemur; pfp, prefemoral process; pg, prostatic groove; r, receptacle; t, tooth; v, valves. Setation is omitted from all illustrations of the 4th sternal process and dissected gonopods.

Sigmoria latior latior (Brolemann) Figs 1-7, 132-133, 139

Fontaria latior Brolemann, 1900:123, pl. 6, figs. 37-42.
Apheloria latior: Attems, 1938:168.
Sigmoria latior: Hoffman, 1950a:5. Chamberlin and Hoffman, 1958:50. Wray, 1967:152
Sigmoria aberrans Chamberlin, 1939:8, pl. 3, figs. 24-25. Hoffman, 1950a:2. Chamberlin and Hoffman, 1958:49. Wray, 1967:152.

Sigmoria conclusa Chamberlin, 1939:8, pl. 3, figs. 22-23. Hoffman, 1950a: 4. Chamberlin and Hoffman, 1958:49. Wray, 1967:152.

Sigmoria furcifera Hoffman, 1949:387, pl. 27, figs. 17-18. Hoffman, 1950a:4. Chamberlin and Hoffman, 1958:50.

Sigmoria latior latior: Shelley, 1976:21, figs. 3, 6-14; 1978:67-68, figs. 71-72.

Type specimen.— The male holotype (MNHP) was taken by an unknown collector as an unknown date from an unspecified location in North Carolina. The MNHP received the specimen from the personal collection of E.L. Simon in Paris, who probably received it as part of a spider collection from North Carolina. Three persons are known to have collected terrestrial arthropods in North Carolina in the late 19th century and are likely collectors of the holotype: George T. Atkinson, who collected the holotype of *Fontaria rubromarginata;* Franklin Sherman, who became state entomologist in 1900 and began the state insect collection (Brimley 1938); and C.S. Brimley, who collected vertebrates and insects in the 1890's and who took charge of the state insect survey in 1919. In 1976 I restricted the type locality to the region of intergradation south of the Deep-Cape Fear Rivers and considered the race in North Carolina north of this boundary the nominate subspecies. The following description therefore is of a male from within the range of the subspecies rather than of the holotype.

Diagnosis.— Paranota varying from red to yellow, metaterga without stripes along caudal edges; gonopods with following diagnostic characters: prefemoral process short, bent at midlength into approximately a right angle, simple or bifurcate; medial flange moderate in size, depth subequal to that of apical curvature; tooth present, subtriangular, located at distal extremity of medial flange; apical curve beginning much closer to tip than to tooth, forming arc with relatively narrow diameter.

Description of Male.— Based on specimen collected by R.L. Hoffman, 11 July 1962, from Burke Co., NC, 4 mi. SE Jonas Ridge, Barkhouse Recreation Area, PNF (RLH). Other species of *Sigmoria,* except for those in the *rubromarginata* and *nigrimontis* groups, will be compared to this description.

Length 42.6 mm, maximum width 11.1 mm, W/L ratio 26.1%, depth/width ratio 57.5%. Segmental widths as follows; those of segments 2-4 are low due to damaged paranota:

collum	7.6 mm	10th-13th	11.1
2nd-3rd	8.2	14th	10.9
4th	8.8	15th	10.5
5th-7th	10.4	16th	10.0
8th-9th	10.7	17th	8.9
		18th	6.6

Color in life: paranota bright lemon yellow, metaterga black; yellow stripe along anterior edge of collum connecting paranotal spots; epicranium dark brown, suture white; frons and genae light brown, clypeus yellow; antennae yellow, ultimate and penultimate segments brown; venter white; legs white basally, other podomeres yellow, claws and distal ends of tarsi brown.

Head capsule smooth, polished, width across genal apices 4.9 mm; interantennal isthmus 1.8 mm, smooth; epicranial suture thin but distinct, terminating in slight impression in interanten-

nal region, not bifid. Antennae moderately long and slender, reaching back to middle of paranota of third segment and becoming progressively more hirsute distally; first antennomere subglobose, 2-6 clavate, 7 short and truncate; relative lengths of antennomeres $2>3>6=4=5>1>7$. Genae not margined laterally, with slight medial impression, ends broadly rounded and projecting slightly beyond adjacent margin of cranium. Facial setae as follows: epicranial, interantennal, and frontal absent; genal 1-1, clypeal about 8-8, labral about 12-12.

Terga smooth, polished, becoming moderately coriaceous on paranota. Collum broad, subequal in width to that of following tergite, caudal edge angled anteriad. Paranota moderately depressed, angled ventrad and continuing slope of dorsum, damaged on right side of segments 2-4; anterior corners of paranota rounded; posterior edge of paranota continuous caudally. Peritremata thick and conspicuous, sharply set off from paranotal surface, produced slightly caudad beginning on segment 7. Ozopores located near middle of peritremata, opening dorsad.

Sides of metazonites irregular, with several shallow, curved impressions. Strictures sharp and distinct. Sternum of segment 4 with very small, double process between 3rd legs, much shorter than width of adjacent coxae (Fig. 1); of segment 5, produced into pair of small, paramedial knobs between 4th pair of legs and two small, elevated flattened areas between 5th legs; of segment 6, convexly recessed between 7th legs to accommodate apical curvature of telopodites. Postgonopodal sterna generally bilobed, produced into small, blunt lobes subtending both pairs of coxae on segments 8-16, with shallow, transverse groove originating between leg pairs; sternal surface smooth, glabrous, slightly depressed between lobes on caudal edge. Pregonopodal legs densely hirsute; postgonopodal legs becoming progressively less hirsute caudally. Small coxal tubercle present on legs of segments 9-17; prefemoral spines beginning on segment 6, becoming progressively longer and sharper caudally, bent apically on some legs; tarsal claws bisinuately curved. Hypoproct rounded, paraprocts with margins strongly thickened.

Gonopodal aperture elliptical, 3.3 mm wide and 1.7 mm long at midpoint, indented on anteriolateral margin, sides slightly raised above metazonal surface. Gonopods *in situ* (Fig. 2, not this specimen) with peaks of acropodites overlapping in midline of aperture, left gonopod ventral to right gonopod, distal portions of peaks projecting forward beyond aperture, distal zones curving dorsomediad and overlapping again in midline. Gonopod structure as follows (Figs. 3-4): coxae moderate in size. Prefemur moderate, with short, bifurcate prefemoral process arising on anterior side, vertical component of process slightly longer and thicker than horizontal component; bent at nearly a right angle at midlength (juncture of two components). Acropodite moderately thick and heavy, arch flattened at peak and extending well beyond level of prefemoral process; basal zone with basal lobe on ventral surface; anterior bend sharp (about 90°), well defined, located at 1/3 length; peak relatively long and flattened, about 1/3 of acropodite length; apical curve sharp and well defined, forming arc with relatively narrow diameter, beginning proximal to tip, much closer to tip than to tooth; distal zone relatively short, curved into arch and directed toward basal zone; tip reflexed. Medial flange broad, margin rounded, arising at anterior bend, extending to about midlength of peak, depth subequal to that of apical curve. Tooth sharply pointed, triangular, located at distal extremity of flange. Lateral flange long and narrow, arising at beginning of apical curve, terminating proximal to tip. Prostatic groove originating in pit at base of prefemur, running along ridge on inner surface of acropodite to opening at end of reflexed tip.

Description of female.— Based on paratype of *aberrans* collected by R.V. Chamberlin, 12 August 1910, from Linville Falls, Burke Co., NC (RVC).

Length 40.0 mm, maximum width 10.7 mm, W/L ratio 26.5%, depth/width ratio 64.5%. Agreeing essentially with male in somatic features except paranota more strongly depressed, creating appearance of more highly arched body; sterna bilobed on segments 5-7, becoming

flat and plate-like in midbody region with wide, shallow, central impressions.

Cyphopodal aperture with edges flush with metazonal surface and slightly thickened. Cyphopods *in situ* with receptacle visible in aperture, valves directed dorsocaudad. Receptacle (Fig. 5) cupped around ventral end of valves, extending about halfway down sides, surface convoluted with numerous low ridges. Valves with surface finely granulate.

Variation.— For a discussion of this topic, the reader is referred to Shelley (1976:24, figs. 6-14).

Ecology.— The nominate subspecies occurs in predominantly deciduous forests, where it may be found under rocks, logs, or thin layers of leaves. The milliped appears to be a potential inhabitant of any hardwood site within its range, whether on a hillside, in a ravine, or in a floodplain.

Distribution.— *Sigmoria latior latior* ranges from southern West Virginia to the Catawba and Deep-Cape Fear Rivers of North Carolina (Fig. 139). It has now been encountered in the Tennessee River drainage area of North Carolina (in the Toe River Basin of Mitchell County) but still not in the Tar and Roanoke basins of North Carolina and Virginia. Specimens were examined from the following new localities (not reported in my 1976 paper):

WEST VIRGINIA: *Mercer Co.,* Athens, old pump house, M, 6 June 1966, W.A. Shear (WAS) and Concord College Campus, F, 5 June 1971, W.A. Shear (WAS).

NORTH CAROLINA: *Alleghany Co.,* 1 mi. S. Roaring Gap, along US hwy. 21, 1.2 mi. W Wilkes Co. line, M, 16 June 1980 (NCSM A3288). *Ashe Co.,* Clifton, M, August 1973, G. Hunt (RLH); 8.5 mi. NE Jefferson, jct. co. rds. 1567 & 1568, M, F, 17 June 1980 (NCSM A3292); and 8.5 mi. W Jefferson, along co. rd. 1100 at Long Hope Cr., M, 17 June 1980 (NCSM A3339). *Avery Co.,* McRae Meadows on Grandfather Mtn., M, 13 July 1975, J.B. Funderburg (NCSM A204). *Mitchell Co.,* 7 mi. N Spruce Pine, near Bakersville, along co. rd. 1206, 0.8 mi. N. jct. co. rd. 1211, M, 21 June 1980 (NCSM A3327). *Wilkes Co.,* Stone Mtn. State Park, M, 2F, 15 July 1975, D.S. Lee and P.T. Hertl (NCSM A285); several localities around Wilkesboro and Morven Falls, MM, FF, August 1975 (NCSM collection); and several localities around Wilkesboro and New Castle, MM, FF, 14-18 July 1976, M. Filka and F.D. Scott (NCSM collection). *Surry Co.,* three localities 5-8 mi. NW Dobson, 14M, 10F, 11 August 1975 (NCSM A443, A450, A453); and Yadkin River section, Pilot Mtn. State Park, M, F, 20 July 1976 (NCSM A933). *Caldwell Co.,* 11.6 mi. ENE Lenoir, along co. rd. 1730, 0.6 mi. S jct. co. rd. 1772, 25M, 2F, 13 August 1975 (NCSM A494); 12 mi. N Lenoir, along co. rd. 1502, 1.5 mi. W jct. co. rd. 1503, 4M, 2F, 22 June 1980 (NCSM A3337); 11 mi. N Lenoir, along co. rd. 1371, 3.0 mi. W jct. co. rd. 1370, M, F, 22 June 1980 (NCSM A3335); and several localities near Kings Creek, MM, FF, 20-21 July 1976, M. Filka and F.D. Scott (NCSM collection). *Alexander Co.,* three localities 4-7 mi. NW Taylorsville, 15M, 7F, 13 August 1975 (NCSM A483, A487, A493); and several localities NE and NW Taylorsville, MM, FF, 19-20 July 1976, M. Filka and F.D. Scott (NCSM collection). *Iredell Co.,* several localities W, SW, and NW New Hope, MM, FF, 19 July 1976, M. Filka and F.D. Scott (NCSM collection); and 9.5 mi. NW Statesville, along co. rd. 1561, 0.5 mi. N. jct co. rd. 1571, M, F, 25 August 1980 (NCSM A3390). *Wake Co.,* Knightdale, M, 24 April 1976, H.W. Levi (NCSM A1021); 7 mi. NNE Raleigh, jct. co. rds. 2218 & 2219 near Neuseoca Lake, M, 23 May 1979, E. Flowers (NCSM A2708); 2.3 mi. ENE Garner, along co. rd. 2548, 1.7 mi. SE jct. co. rd. 2547, M, 10 June 1979, A.L. Braswell (NCSM A2725); and Raleigh, dead in Dover Rd. near Chester St., M, 24 June 1980 (NCSM A3338).

Remarks.— In addition to new locality records, field collecting of *l. latior* also produced a male with a bizarre gonopodal anomaly which was described as a heteromorphosis by Shelley (1977b). Both appendages on the right side of segment 7 are abnormal, but the anterior one exhibits both gonopodal and ambulatory characteristics (Figs. 6-7). It has a normal gonopodal coxa, complete with apodeme and cannula, but the remaining podomeres are leglike though considerably reduced in size. I believe that this mixed leg-gonopod, occurring at the normal reproductive position, is the best evidence available that a gonopod is a modified leg which is highly specialized for a copulatory function.

During field work in western North Carolina in May 1978 and June 1980, I tried to resolve the identity of *Sigmoria aberrans* by seeking topotypes around Linville Falls, both the Falls themselves and the community on US highway 221. No specimens were found, but it still seems probable, for reasons previously given (Shelley 1976), that this combination is a synonym of *l. latior*. A less important problem concerns the type locality of *conclusa,* also a synonym of *l. latior*. In June 1980 a male of this subspecies was discovered in Mitchell County near Bakersville (7 mi. N Spruce Pine), some 9.5 miles NW Altapass, the purported type locality of *conclusa* (see discussion in Shelley 1976). This specimen is the first authentic one ever collected in the Tennessee River drainage area of North Carolina and lends credence to Chamberlin's report (1939) of a specimen from Altapass, in southern Mitchell County.

Sigmoria latior munda Chamberlin, new status Figs. 8, 132-133, 137, 139

Sigmoria munda Chamberlin, 1939:8, pl. 2, figs. 15-16. Hoffman, 1950a:6. Chamberlin and Hoffman, 1958:51. Wray, 1967:152.

Sigmoria mariona Chamberlin, 1939:9, pl. 2, figs. 17-18. Hoffman, 1950a:6. Chamberlin and Hoffman, 1958:50. Wray, 1967:152. **NEW SYNONYMY.**

Sigmoria latior mariona: Shelley, 1976:28-29, fig. 4.

Apheloria brachygon[3] Brimley, 1938:498.

Sigmoria brachygon Chamberlin, 1940a:283-284, fig. 2. Hoffman, 1950a:3. Chamberlin and Hoffman, 1958:49. Wray, 1967:152. **NEW SYNONYMY.**

Type specimens.— Male holotype (RVC) and two male paratypes collected by R.V. Chamberlin, 6 August 1910, from Hot Springs, Madison Co., NC.

[3]This binomial is accompanied by the notation "Pisgah Forest, June," and undoubtedly refers to *Sigmoria brachygon,* the type of which was collected at Glen Bald, Pisgah National Forest, Buncombe County, on June 3, 1933. However, *S. brachygon* was published in 1940, two years after Brimley's list, and since no descriptive information was provided, *A, brachygon* is a *nomen nudum*. Chamberlin is cited as a contributor to Brimley's list for his determinations of myriapods, and it seems that *A. brachygon* was communicated to Brimley by Chamberlin prior to the time that he decided to divide *Apheloria* into several genera.

Diagnosis.— Paranota usually yellow, occasionally red, metaterga with concolorous transverse strips along caudal edges connecting paranotal spots; gonopods with following diagnostic characters: prefemoral process varying but usually relatively long and bifurcate, vertical component usually more prominent than horizontal component; medial flange moderate in size, depth subequal to or slightly less than that of apical curve of acropodite; tooth absent; apical curve beginning approximately midway between tip and flange (or tooth location), forming arc with moderate diameter.

Ecology.— As with the nominate subspecies, *l. munda* inhabits moist deciduous forests in general.

Distribution.— The range of *l. munda* is much greater than I realized in 1976. Only three localities in McDowell, Polk, and Transylvania counties, North Carolina, were cited then for a range described as the eastern edge (Atlantic drainages) of the mountains of southwestern North Carolina. Now the race is known from lowland areas in the western Piedmont of both Carolinas as well as around the French Broad and Little Tennessee rivers in western North Carolina. However, it is rare west of the eastern continental divide and will only be encountered occasionally; it may eventually be discovered in Cocke County, Tennessee, as Hot Springs is only six miles from the state line. The range can now be described as the French Broad and upper Little Tennessee drainage areas of western North Carolina to the western Piedmont of North and South Carolina, or from Madison County, North Carolina, to Cherokee and Spartanburg counties, South Carolina (Fig. 139). Specimens were examined from the following new localities (not reported in my 1976 paper):

NORTH CAROLINA: *Madison Co.,* Hot Springs, 4M, 6 August 1910, R.V. Chamberlin (RVC) TYPE LOCALITY. *Yancey Co.,* 5.8 mi. WSW Burnsville, along co. rd. 1128, 0.2 mi. S. jct. US hwy. 19, M, 2F, 20 July 1975 (NCSM A426). *Jackson Co.,* Speedwell Rd. near Cullowhee, M, 7 May 1971, R. Harburn (NCSM A2115). *Buncombe Co.,* Glen Bald, Bent Creek Forest Experiment Station, PNF, M, 3 June 1933, A.S. Pearse (RVC); and Asheville, M, July 1896, collector unknown (NMNH). *Macon Co.,* Otto, sawdust piles, 2M, F, 16 September 1959, W. Suter (FSCA). *Polk Co.,* 6 mi. SW Sunny View, along co. rd. 1155, 1 mi. W jct. co. rd. 1138, M, 7 June 1978 (NCSM A2036). *Rutherford Co.,* 5.3 mi. SW Caroleen, along US hwy. 221, 0.3 mi. S jct. co. rd. 2109, M, 2F, 15 August 1975 (NCSM A528); 6.9 mi. SW Forest City, along co. rd. 1148, 0.9 mi. E jct. co. rd. 1005, M, 15 August 1975 (NCSM A529); 2.8 mi. SW Rutherfordton, along NC hwy. 108, 1.5 mi. W jct. co. rd. 1161, 3M, F, 15 August 1975 (NCSM A532); and 3 mi. SW Rutherfordton, beech-maple woods, M, 3 October 1953, L. Hubricht (RLH).

SOUTH CAROLINA: *Cherokee Co.,* 10 mi. S. Gaffney, along SC hwy. 15 at Thicketty Cr., M, 10 May 1977 (NCSM A1484); and 4.6 mi. SE Blacksburg, along SC hwy. 5, 0.3 mi. S jct. SC hwy. 68, F, 10 May 1977 (NCSM A1483). *Spartanburg Co.,* 2.7 mi. S Pacolet, along SC hwy. 150 at Ison's Cr., 2M, 13 June 1978 (NCSM A2077); and 6 mi. N Woodruff, along SC hwy. 197 at S. Tyger River, 2M, 2F, 13 June 1978 (NCSM A2079).

Remarks.— The color of montane specimens is black with yellowish paranota and yellowish stripes along the caudal margins of the metaterga. This was the color of the material from Yancey County, and a notation with the non-type male from Hot Springs states, "margins yellow." Because of these yellow stripes, *l. munda* should be readily indentified in the mountains on those rare times it is encountered, as most of the other "sigmoid" xystodesmids have red stripes, and *Apheloria* is spotted. The only xystodesmids which might be confused with *l. munda* are *Sigmoria areolata,* which also has yellow stripes, and forms of *Cherokia,* a rhysodesmine genus which displays yellowish stripes in certain areas. The latter, however, has different body proportions, long straight gonopods, and prominent acute lobes on the caudal margins of the sterna. The color of *l. munda* varies in the Piedmont. Specimens from Rutherford County, North Carolina, and Cherokee County, South Carolina, had yellow paranota and stripes, whereas the individuals from Spartanburg County, had red markings.

Sigmoria latior hoffmani Shelley Figs. 9, 137, 139

Sigmoria latior hoffmani Shelley, 1976:29, fig. 5.

Type specimen.— Male holotype (RLH) collected by L. Hubricht, 14 May 1960, from upland mixed woods, 4.4 mi. NW North, Orangeburg Co., SC.

Diagnosis.— Paranota red, metaterga black with reddish transverse stripes along caudal edges connecting paranotal spots; gonopods with following diagnostic characters: prefemoral process moderately long and simple, not bifurcate; medial flange greatly enlarged, depth greater than that of apical curve of acropodite, extending to near level of prefemoral process; tooth present but variable in size and configuration, separated slightly from distal extremity of flange; apical curve beginning closer to tooth than to tip, forming arc with relatively broad diameter.

Ecology.— I have encountered this subspecies under thin layers of leaves on relatively hard substrates, often in association with *Pachydesmus crassicutis incursus* Chamberlin. It is not uncommon on wet soil at the edges of cypress swamps, but avoids places where there is standing water. At Edisto Beach State Park, Charleston-Colleton counties, South Carolina, individuals were found in live oak litter on sand dunes near the camping area, only a few meters from the high water mark of the Atlantic Ocean.

Distribution.— The range of this subspecies is the Coastal Plain of southern South Carolina between the Savannah and Congaree-Santee Rivers (Figs. 137, 139). The Edisto Beach State Park specimens confirm its existence in the tidewater region (outer Coastal Plain). I have searched un-

successfully for the diplopod south of the Savannah River in Georgia, and its range appears to end at this natural boundary. Specimens were examined from the following new localities (not reported in my 1976 paper):

SOUTH CAROLINA: *Berkeley Co.,* Bonneau, M, summer 1929, O.F. Cook (NMNH); and along SC hwy. 402 near Huger Recreation area, M, 2F, 11 September 1980 (NCSM A3502). *Charleston Co.,* James Island, M, date and collector unknown (NMNH); Hampton Plantation State Park, M, F, 11 September 1980 (NCSM A3503); and Bear Bluff on Wadmalaw Island, M, F, 11 September 1980 (NCSM A3504). *Bamberg Co.,* Rivers Bridge State Park, M, 7 August 1976 (NCSM A1382); and 10 mi. S Bamberg, along US hwy. 601, in rotten leaves, 2M, 4F, 18 August 1961, D. Dowling (FSCA). *Dorchester Co.,* Givhans Ferry State Park, 2M, 10 September 1980 (NCSM A3499); Old Dorchester State Park, M, F, 10 September 1980 (NCSM A3500); and Francis Beidler Forest near Harleyville, 4M, F, 9 September 1980 (NCSM A3491). *Barnwell Co.,* Barnwell State Park, 7M, 4F, 7 August 1976 (NCSM A1384). *Colleton Co.,* Colleton State Park, 2M, F, 10 September 1980 (NCSM A3497); and Edisto State Park, 5M, F, 12 September 1980 (NCSM A3506). *Orangeburg Co.,* Orangeburg, beneath oak in roots of ivy, 3M, 4F, 23 June 1961, D. Dowling (FSCA) and 6M, 8F, July 1961, D. Dowling (FSCA); and Santee State Park, M, 2F, 9 September 1980 (NCSM A3495). *Saluda Co.,* 11 mi. NNE Saluda, along SC hwy. 39, 2M, 2F, 14 July 1979 (NCSM A2807); 6 mi. NW Saluda, along SC hwy. 114, 1.5 mi. NE jct. SC hwy. 39, 2M, 2F, 14 July 1979 (NCSM A2808); and along US hwy. 178 at Little Saluda Cr. in Saluda, M, 15 July 1979 (NCSM A2809); *Edgefield Co.,* 12 mi. N Edgefield, along SC hwy. 24 at Sleepy Cr. 2M, 2F, 4 May 1977 (NCSM A1529); *Greenwood Co.,* Greenwood State Park, M, 9 August 1976 (NCSM A1389).

Sigmoria latior intergrades Figs. 132, 137, 139

In 1976 I attemped to distinguish between types of intergrades, but having now found many more intergrade specimens and much more variation than previously known, I realize that this is not feasible. Consequently, intergrade material of all types is included in the locality citations below. As noted earlier, specimens with the solid metatergal color pattern of the nominate subspecies have now been collected from Lincoln, Cleveland, and Mecklenburg counties, North Carolina, and Chester County, South Carolina. In my 1980 revision of *Pleuroloma* I reported that *Apheloria tigana* Chamberlin and *Pleuroloma pinicola* Shelley were the only xystodesmid species in the Coastal Plain of North Carolina. The discovery of *latior* intergrades in southeastern North Carolina (Robeson and Brunswick counties) now brings the total to three species, so all the xystodesmids that would be expected in the region actually occur there.

Distribution.— The general area of intergradation — central Carolinas around their common border (Fig. 139) — is slightly narrower than reported in 1976 due to the discovery of *l. munda* in the western Piedmont. Some overlap with this subspecies occurs in Spartanburg County, South Carolina, as the male listed here from Croft State Park is a definite intergrade with a small but distinct tooth, whereas the specimens listed under *l. munda* lack this character. One new record deserving special mention is that from Horry County, South Carolina. The male from this locality is

unique in lacking the tooth while displaying a typical intergrade flange, prefemoral process, and apical curve of the acropodite. Only one male has been collected there; a subsequent trip to Galivant's Ferry in March 1979 was unproductive. Collections of intergrade specimens in Robeson and Brunswick counties, North Carolina, establish *latior* much farther east in the Coastal Plain of this state than previously known; the site in Brunswick County is only about 25 miles from the Atlantic Ocean. Unlike the Horry County male, however, the coastal North Carolina males possess a tooth on each gonopod. Specimens were examined from the following new localities (not reported in my 1976 paper):

NORTH CAROLINA: *Brunswick Co.,* 5.8 mi. N Maco, in hardwood litter in ravine on Cape Fear River, M, 16 October 1979 (NCSM A2917). *Robeson Co.,* 1.3 mi. NNW St. Pauls, Rest Area on I-95 just N jct. NC hwy. 20, M, F, 23 March 1979 (NCSM A2521). *Moore Co.,* 2.9 mi. SE Southern Pines, along co. rd. 2141, 0.6 mi. S jct. co. rd. 2110, M, 27 September 1975, M.R. Cooper (NCSM A583). *Hoke Co.,* 12-13 mi. NW Raeford, along co. rd. 1125, 0.8 mi. E jct. US hwys. 15-501, 2M, 14 December 1977, A.L. Braswell and R.E. Ashton (NCSM A1816). *Scotland Co.,* 4.5 mi. N Laurinburg, along US hwys. 15-501, 0.4 mi. N jct. co. rd. 1323, 2F, 8 September 1980 (NCSM A3488). *Richmond Co.,* 4 mi. NW Ellerbe, along NC hwy. 73, M, 2F, 15 July 1975 (NCSM A208). *Union Co.,* 4.8 mi. S. Waxhaw, along co. rd. 1106, 0.1 mi. S jct. co. rd. 1194, M, 23 August 1977 (NCSM A1633); and along NC hwy. 200, 0.2 mi. S jct. co. rd. 1114, 2M, F, 15 September 1980 (NCSM A3516). *Mecklenburg Co.,* 1.5 mi. E Pineville, along US hwy. 521, 0.3 mi. E jct. co. rd. 3627, M, 23 August 1977 (NCSM A1635). *Burke Co.,* 4.8 mi. SE Morganton, along co. rd. 1922, 0.4 mi. S jct. co. rd. 1936, 2M, 26 July 1975 (NCSM A347); and 9.2 and 10.4 mi. S Valdese, along co. rds. 1900 and 1904, 3M, F, 14 August 1975 (NCSM A510, A511). *McDowell Co.,* along NC hwy. 80, 3.2 mi. S jct. Blue Ridge Pkwy., 2M, 20 July 1975 (NCSM A422). *Catawba Co.,* 6.4 mi. SW Hickory along co. rd. 1002 at Jacob Fork R., 2M, 2F, 14 August 1975 (NCSM A504); 7.3 mi. S Hickory, along NC hwy. 10 at S. Fork Catawba R., 6M, 3F, 14 August 1975 (NCSM A519); and 9.5 mi. SE Newton, summit of Anderson Mtn., M, F, 26 August 1980 (NCSM A3394). *Lincoln Co.,* 7.2 mi. E Lincolnton, along NC hwy. 73, 0.7 mi. E jct. co. rd. 1509, 2M, 25 July 1976 (NCSM A982); 14.5 mi. E Lincolnton, along NC hwy. 73, 0.6 mi. W jct. co. rd. 1386, M, 26 August 1980 (NCSM A3396); and 6.5 mi. S Lincolnton, along co. rd. 1190, 0.8 mi. S jct. NC hwy. 27, M, 25 July 1976 (NCSM A983). *Cleveland Co.,* 2.1 mi. W Casar, along co. rd. 1536, 1.4 mi. W jct. co. rd. 1538, 6M, 6F, 14 August 1975 (NCSM A516); 2 mi. SW Fallston, jct. co. rds. 1803 & 1805, 2M, F, 14 August 1975 (NCSM A521); and 4.1 mi. SW Kings Mountain (town), along co. rd. 2245, 2 mi. NW jct. co. rd. 2283, 7M, 2F, 16 August 1975 (NCSM A536). *Gaston Co.,* Lowell, along co. rd. 2201, 1.2 mi. N jct. NC hwy. 7, 4M, 2F, 29 April 1976 (NCSM A714); 4.8 mi. NE Gastonia, along co. rd. 2201, 1.5 mi. N jct. NC hwy. 7, 15M, 2F, 7 July 1976, M. Filka and W.W. Thomson (NCSM A1038); and base of Spencer Mtn. near town of Spencer Mountain, M, 10 April 1977, M. Filka (NCSM A2175).

SOUTH CAROLINA: *Horry Co.,* Galivant's Ferry, M, 22 March 1952, collector unknown (RLH). *Lee Co.,* Lee State Park, M, F, 8 September 1980 (NCSM A3490). *Chesterfield Co.,* Cheraw, M, 18 July 1958, K. Dawson (FSCA); and 4 mi. N Chesterfield along SC hwy. 145, 2M, 12 July 1979 (NCSM A2780). *Lancaster Co.,* 12 mi. WSW Heath Springs, along SC hwy. 20 at Catawba R., 2M, 12 July 1979 (NCSM A2784). *Chester Co.,* Chester State Park, 4M, F, 4 August 1976 (NCSM A1374); Woods Ferry Recreation Center on Broad R., Sumter National Forest, 8M, F, 4 August 1976 (NCSM A1378); 7.2 mi. ESE Chester, along SC hwy. 44, 0.7 mi.

W jct. SC hwy. 347, 3M, 1 May 1977 (NCSM A1490); Landsford Canal State Park, 2M, 1 May 1977 (NCSM A1496); and 11.2 mi. NE Chester, along SC hwy. 32, 0.7 mi. N jct. SC hwy. 46, 2M, 1 May 1977 (NCSM A1497). *Union Co.,* 12.3 mi. SE Union, along SC hwy. 121 at Cane Cr., 3M, 2F, 5 August 1976 (NCSM A1379); 0.1 mi. N Jonesville, along SC hwy. 18, M, 2 May 1977 (NCSM A1506); and 5 mi. N Carlisle, along SC hwy. 86 at Neal's Cr., 3M, F, 2 May 1977 (NCSM A1515). *Spartanburg Co.,* Croft State Park, M, 9 May 1977 (NCSM A1628). *Fairfield Co.,* 13 mi. SW Winnsboro, along SC hwy. 46 at Sawney's Cr., M, F, 13 July 1979 (NCSM A2787); and 9 mi. NE Winnsboro, along SC hwy. 234 at Wateree Cr., M, F, 13 July 1979 (NCSM A2790).

Remarks.— Filka and Shelley (1980b) examined the gonopod primordia of intergrades from Gaston and Cleveland counties, North Carolina, under the scanning electron microscope and found important similarities and differences between these structures and those of the polydesmids, *Polydesmus angustus* Latzel and *Brachydesmus superus* Latzel. They concluded that juvenile developmental stages may be more useful in phylogenetic considerations than previously thought, and that further application of scanning electron microscopy to millipeds was warranted.

Sigmoria stenoloba, new species Figs. 10-18, 132-133

Type specimens.— Male holotype (NCSM A457) and 17 male and 13 female paratypes collected by R.M. Shelley and J.C. Clamp, 11 August 1975, from Wilkes Co., NC, 7.8 mi. NNE North Wilkesboro, in Roaring River Township, along NC hwy. 268 at junction of county road 2083. Male and female paratypes deposited in FSCA and RLH.

Diagnosis.— A moderate-size species of *Sigmoria* with medial flange on proximal portion of peak and with red to yellow paranota but without complete stripes along caudal margins of metaterga; gonopods with following diagnostic characters: prefemoral process short, rarely bifurcate; basal zone with basal lobe on ventral surface; apical curve distinct, forming arc with relatively broad diameter, beginning much closer to tooth than to tip; medial flange long and narrow, beginning at base of anterior bend, terminating about midlength of peak, depth less than that of apical curve; tooth highly variable, often greatly reduced and rounded.

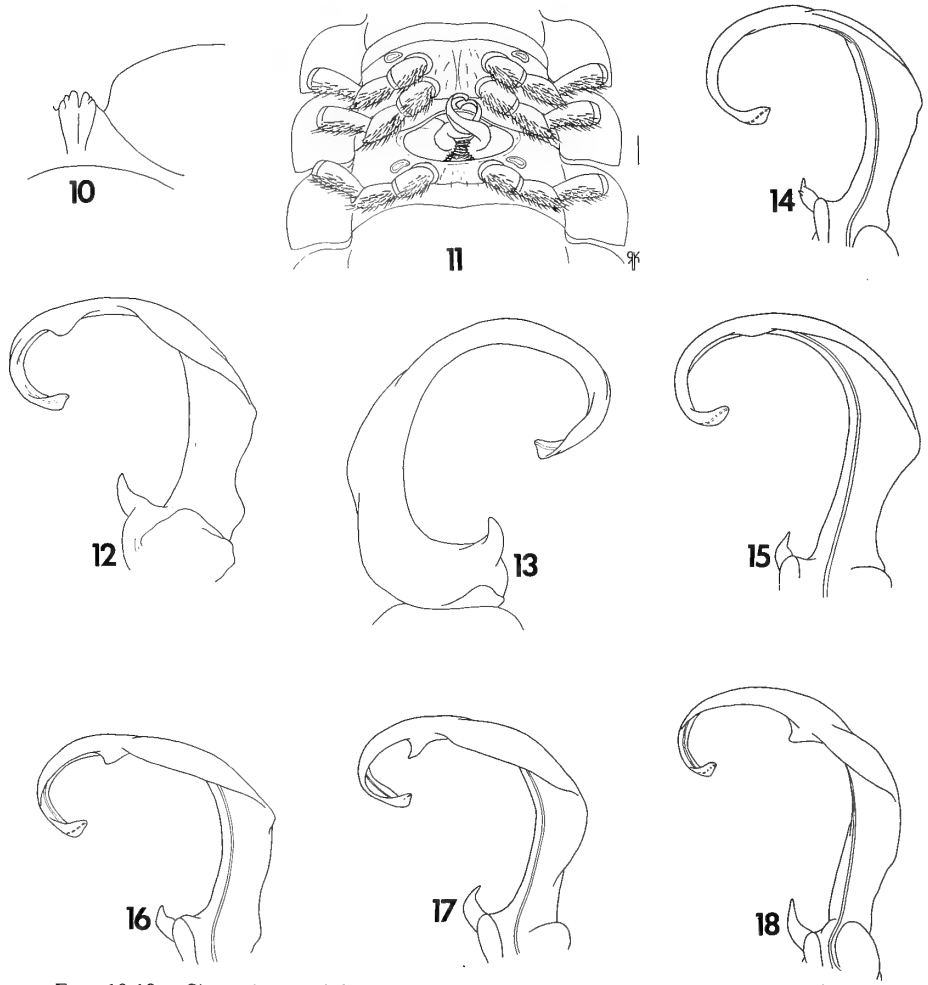
Holotype.— Length 38.6 mm, maximum width 9.9 mm, W/L ratio 28.3%, depth/width ratio 54.5%. Segmental widths as follows:

collum	6.5 mm	12th-14th	9.9
2nd	7.9	15th	9.2
3rd	8.7	16th	8.7
4th-7th	9.2	17th	7.8
8th-11th	9.8	18th	5.0

Color in life: Paranota reddish with color extending mediad slightly along caudal edges of metaterga; metaterga black, without complete stripes along caudal edges; collum with narrow reddish stripe along anterior edge connecting paranotal spots.

Somatic features similar to those of *I. latior,* with following exceptions:

Width across genal apices 4.6 mm, interantennal isthmus 1.7 mm. Antennae longer, extending backwards to middle of 4th segment; relative lengths of antennomeres 2>3>4>6=5>1>7. Facial setae as follows: epicranial and interantennal absent, frontal 1-1,



FIGS. 10-18, *Sigmoria stenoloba.* 10, process of 4th sternum of holotype, caudal view. 11, gonopods *in situ,* ventral view of specimen from 0.8 mi. N North Wilkesboro, Wilkes Co., North Carolina. 12, telopodite of left gonopod of holotype, medial view. 13, the same, lateral view. 14, telopodite of left gonopod of specimen from 3.1 mi. N North Wilkesboro, medial view. 15-17, telopodites of left gonopods of specimens from 1.6 mi. N North Wilkesboro, medial views. 18, telopodite of left gonopod of specimen from 3.4 mi. W Conover, Catawba Co., North Carolina, medial view. Scale line for fig. 11 = 1.00 mm; line for other figs. = 1.00 mm for each.

genal 1-1, clypeal about 8-8, labral about 12-12, merging with clypeal series and continuing for short distance along borders of genae, about 4 setae on genal border on each side.

Collum extending slightly beyond ends of following tergite, caudal edge relatively straight. Paranota relatively flat, interrupting slope of dorsum.

Processes of pregonopodal sterna closely similar to those of *l. latior;* 6th sternum convexly recessed between 7th legs to accommodate curvature of acropodites, 7th legs set slightly farther apart than 6th. Postgonopodal sterna with small blunt lobes on segments 8-15; surface smooth, glabrous, with varying shallow impressions.

Gonopodal aperture subelliptical, 3.1 mm wide and 1.2 mm long at midpoint, indented on anteriolateral margin, sides flush with metazonal surface, caudal margin with faint medial lobe. Gonopods *in situ* (Fig. 11, not this specimen) with telopodites overlapping at about midlength in midline, projecting forward over anterior margin of aperture to between 7th legs, apices curving towards each other and crossing. Gonopod structure as follows (Figs. 12-13): prefemoral process short and acuminate, not bifurcate, directed approximately toward midlength of acropodite. Acropodite moderately thick, arch extending well beyond level of prefemoral process; basal zone with basal lobe on ventral surface; anterior bend sharp and well defined, about 90°, located at about 1/3 length; peak relatively long and flat, about 1/3 of acropodite length; apical curve broad, forming arc with relatively wide diameter, beginning closer to tooth than to tip; distal zone moderately long, curved broadly into arch, directed toward basal zone; tip reflexed. Medial flange narrow, barely obscuring acropodite stem, depth less than that of apical curve, arising at anterior bend and extending to about midlength of peak. Tooth rounded, well separated from distal extremity of medial flange. Lateral flange long and narrow, arising near beginning of apical curve and terminating proximal to tip. Prostatic groove running along inner surface of acropodite to opening on reflexed tip.

Male paratypes.— The male paratypes vary greatly in body dimensions as shown in the following table. Only 12 individuals were measurable; the others were badly fragmented.

Width (mm)			Length (mm)			W/L (%)	
Range	$\bar{x}$	s	Range	$\bar{x}$	s	Range	$\bar{x}$
9.1-10.6	10.0	7.40	37.4-44.1	41.2	2.27	22.7-26.5	24.3

The shape of the dorsum also varies considerably. The paranota of the smaller individuals (less than 40 mm long) are generally much flatter than those of larger specimens.

The caudal edge of the aperture is raised in the midline to form a rounded lobe in some specimens, whereas in others it is virtually flat. The condition in the holotype is about midway between these two extremes. As with *l. latior* the tips of the telopodites cross on some males so that the gonopods form a single interlocking unit.

On the gonopods the prefemoral processes and degree of apical curvature of the acropodite are rather consistent, although the former are thinner and more acute on some individuals. The flange and tooth are the most variable aspects, and the former is practically absent from some males, being represented only by a slight expansion at the anterior bend. In these individuals the flange does not obscure any of the stem of the acropodite. The holotype has one of the larger flanges in the type series, which range from this configuration to nearly absent. A similar situation exists with respect to the tooth. It is nearly absent from some paratypes, being only a low callus on the blade of the acropodite, but in others it is acutely triangular and resembles the tooth of *l. latior*. Again, the condition in the holotype is approximately intermediate between these two extremes. No correlation is possible between the configurations of the tooth and flange, and it is possible to have any size tooth with a given size flange.

Female paratype.— Length 44.4 mm, maximum width 10.1 mm, W/L ratio 22.8%, depth/width ratio 62.4%. Agreeing essentially with holotype in somatic features, with follow-

ing exceptions: paranota strongly depressed, angled sharply ventrad, producing appearance of more highly arched body; anterior segments noticeably narrower, widest around segment 11 with sides parallel thereafter to caudalmost segments; collum not as wide as succeeding segment.

Cyphopods *in situ* with side of receptacle visible in aperture, valves directed caudolaterad. Receptacle large, extending around lateral side of valves, surface convoluted with ridges. Valves moderately large and subequal, surface with ridges.

Variation: The color of *stenoloba* varies in much the same way as that of *l. latior* (Shelley 1976). The paranota may be red, pink, orange, or yellow, and one female paratype was nearly completely black, with only the peritremata colored. Specimens from northern Wilkes County in the vicinity of Traphill and Stone Mountain State Park, appear to be striped, as the paranotal indentations on the caudal edge nearly meet in the midline. These individuals therefore resemble the red striped species of *Sigmoria* occurring in the Blue Ridge Province. The postgonopodal sterna of most males have a less lobed appearance than those of the holotype, being flat and unmodified, with small lines of setae adjacent to the leg coxae on segments 8-11.

The gonopods vary as described above for the male paratypes. Specimens from the southern part of the range in Catawba County have larger flanges than those from Wilkes County and might represent a second race or perhaps even another species (see Remarks section).

Ecology.— *Sigmoria stenoloba* inhabits a different environment than does *l. latior* in parts of Wilkes and Catawba counties where they are sympatric, and the two millipeds are not microsympatric as they have never been collected together at a site. Both occur in predominantly hardwood forests, but there are subtle differences between localities where each is found. *Sigmoria latior* lives in the best climax forest habitat available, where the litter and humus layers are thickest and there is little understory and few herbaceous plants. *Sigmoria stenoloba,* however, occurs in disturbed areas, places with considerable pine, or localities where the substrate is inferior. For example, I have collected *stenoloba* in litter under blackberry briars, a place where few other millipeds can be found, and in Catawba County I discovered it in two small hardwood tracts along a newly constructed segment of I-40 which had been used as a fill area for dirt excavated for the highway. The site was very dry and dusty, but *stenoloba* was there on extremely hard, rocky substrate. Thus, *stenoloba* and *latior* are ecologically isolated in distinct deciduous forest environments.

Distribution.— Foothills and western Piedmont Plateau of North Carolina, from northern Wilkes to central Catawba counties (Fig. 132). No specimens have been found in the area between these populations. Specimens were examined as follows:

NORTH CAROLINA: *Wilkes Co.,* Stone Mountain State Park, M, 21 June 1978, A.L. Braswell and W. Lazar (NCSM A2147); 2.1 mi. WSW Traphill, along co. rd. 1742, 0.2 mi. N jct. co. rd. 1002, 4M, 2F, 2 June 1978, A.L. Braswell and W.M. Palmer (NCSM A2025); 7.2 mi. NW North Wilkesboro, along co. rd. 1541, 0.1 mi. E jct. co. rd. 1544, 11M, 4F, 12 August 1975 (NCSM A467); 7.8 mi. NNE North Wilkesboro, Roaring River Twp., jct. NC hwy. 268 and co. rd. 2083, 18M, 13F, 11 August 1975 (NCSM A457) TYPE LOCALITY; 3.1 mi. N North Wilkesboro, along co. rd. 1534, M, 23 July 1973 (NCSM 1871); 1.3 mi. NNW North Wilkesboro, along ext. co. rd. 1517 along N bank Reddies R., 3M, 4F, 23 July 1973 (NCSM 1858) and 5M, 4F, 11 August 1975 (NCSM A460); and 0.8 mi. N North Wilkesboro, along co. rd. 1502, 0.2 mi. S jct. co. rd. 1517, 5M, 4F, 2 August 1975 (NCSM A463). *Catawba Co.,* 3.4 mi.W Conover, M, 23 June 1951, L. Hubricht (RLH); 3.6 mi. SE Hickory, along co. rd. 1468, jct. US hwy. I-40, 2M, 13 August 1975 (NCSM A502); 4 mi. ESE Hickory, along co. rd. 1692, 0.2 mi. W jct. co. rd. 1476, M, 13 August 1975 (NCSM A503); and 1.3 mi. E Claremont, along US hwy. 64-70, 3M, 26 August 1980 (NCSM A3392).

Remarks.— Sigmoria stenoloba can be easily confused with the sympatric *l. latior* or *latior* intergrades, and in their common range identifications should be based on several gonopodal characters in combination rather than single features. The absence of material between Wilkesboro and Hickory is puzzling, expecially considering how common *stenoloba* is north of Wilkesboro. I have investigated many substandard environments in Alexander County without success, and the Brushy Mountains in southern Wilkes County have likewise been thoroughly sampled by personnel of the NCSM. The existence of a population near Hickory is equally mystifying, as this is south of the Catawba River, which would be a logical boundary for the species and is, in fact, the southern limit for *l. latior.* The Catawba population is apparently quite small, as specimens have only been found in or near a restricted area along I-40; none have been collected farther south in Catawba County or in the nearby South Mountains.

Some might argue that *stenoloba* is merely an ecotype or ecophenotype of *l. latior;* however, it has its own geographic range and its own set of anatomical characters, which vary between different parameters than do those of *l. latior. Sigmoria stenoloba* does not occur in substandard habitats throughout the range of *l. latior;* it occurs only in Wilkes County, North Carolina. Were this form an ecotype or ecophenotype of *l. latior* it would be expected in the same habitats in West Virginia, Virginia, and especially the eastern Piedmont of North Carolina, which has abundant marginal environments. Consideration of all these factors leads me to the conclusion that the form with the narrow flange is a true species, reproductively isolated from *l. latior. Sigmoria stenoloba* appears to be recently evolved and is clearly closely related to *l. latior.* It probably arose from a population of the latter which became ecologically isolated in substandard environments.

The status of the Catawba population is uncertain. I include it here with *stenoloba,* but it could also be a separate species, as the flanges are broader

than those of the northern population, and the gonopods demonstrate less variability. For example, the gonopods of the seven males from Catawba County are much more uniform than those of any seven males in the type series. Hence, similarities between the Wilkes and Catawba populations could represent convergence, and the narrow flange could have arisen independently from *l. latior* in Wilkes County and *latior* intergrades in Catawba County. Whereas I think that the Wilkes population is a distinct species, as explained in the preceding paragraph, the Catawba County forms could be ecotypes or ecophenotypes of *latior* intergrades. I leave a final decision on this matter to future investigators, who can secure more material from Catawba County and gain a more confident knowledge of the presence or absence of *stenoloba* in Alexander County.

Sigmoria areolata, new species Figs. 19-22, 132-133

Type specimens.— Male holotype (NCSM A1716) and 3 male and 3 female paratypes collected by R.M. Shelley, 9 September 1977, from Buncombe Co., NC, 7 mi. SE Asheville, along county road 3121, 0.1 mi. W junction of county road 3119. One male and 5 female paratypes taken at same locality by same collector on 8 September 1977. Male and female paratypes deposited in FSCA.

Diagnosis.— A moderate-size species of *Sigmoria* with medial flange on proximal portion of peak and with yellow paranota and yellow stripes along caudal edges of metaterga; gonopods with following diagnostic characters: prefemoral process relatively long, usually apically bifurcate; anterior bend and apical curve sharp, latter forming poorly defined arc; peak not flattened, flexed ventrad with apex at midlength; distal zone straight, angled slightly into arch, subtending about 45° angle with peak; tip simple; medial flange distinct, with varying subrounded lobe; tooth present, variable in size and configuration, well separated from lobe of flange but attached to same lamina; lateral flange present, usually expanded and lobe-like.

Holotype.— Length 39.7 mm, maximum width 8.8 mm, W/L ratio 22.2%, depth/width ratio 62.5%. Segmental widths as follows:

collum	5.9 mm	14th-15th	8.5
2nd	7.2	16th	8.0
3rd	7.7	17th	7.0
4th-8th	8.5	18th	5.3
9th-13th	8.8		

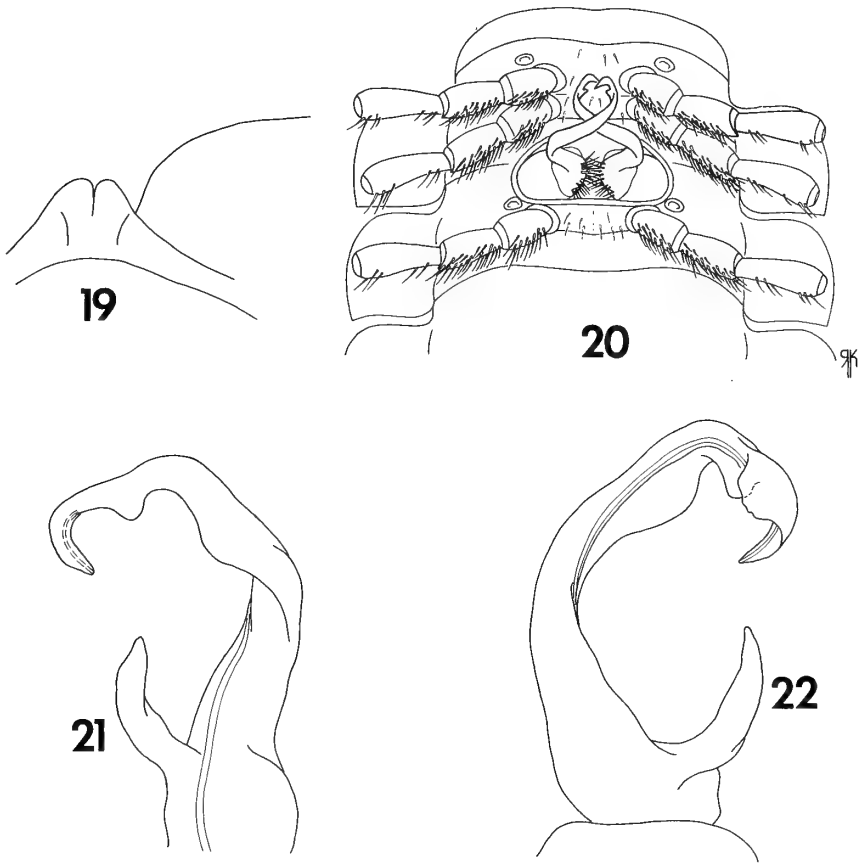
Color in life: paranota bright lemon yellow; metaterga with wide yellow stripes along caudal margins connecting paranotal spots; collum with yellow stripes along both anterior and caudal margins.

Somatic features similar to those of *l. latior,* with following exceptions:

Width across genal apices 4.6 mm, interantennal isthmus 1.9 mm. Frons with wide, shallow impression. Antennae extending back to caudal edge of third segment, relative lengths of antennomeres 2>3>5=6>4>1>7. Facial setae as follows: epicranial 1-1, interantennal absent, frontal 1-1, genal absent, clypeal about 8-8, labral about 12-12, merging with clypeal series and continuing for short distance, along genal borders, about 4 setae on each side.

Dorsum very glossy. Collum extending slightly beyond ends of following tergite. Caudal margins of all tergites relatively straight.

Process of 4th sternum (Fig. 19) very small; paramedial knobs and flattened areas of the 5th sternum reduced over condition in *l. latior;* sternum of segment 6 as in *l. latior.* Postgonopodal sterna generally without lobes on caudal edges, with varying shallow grooves and impressions on surface. Coxal tubercles very small, indistinct.



FIGS. 19-22, *Sigmoria areolata.* 19, process of 4th sternum of holotype, caudal view. 20, gonopods *in situ,* ventral view of paratype. 21, telopodite of left gonopod of holotype, medial view. 22, the same, lateral view. Scale line for fig. 20 = 1.00 mm; line for other figs. = 1.00 mm for each.

Gonopodal aperture ovoid, 2.9 mm wide and 1.4 mm long at midpoint, indented on anteriolateral margin, sides flush with metazonal surface. Gonopods *in situ* (Fig. 20, of paratype) with acropodites overlapping at midlength in midline of aperture, tips curved back toward each other and crossing slightly, extending forward well beyond anterior edge of aperture and over 6th sternum. Gonopod structure as follows (Figs. 21-22): prefemoral process long, curved ventrad at midlength and directed toward midlength of acropodite. Acropodite moderately thick and heavy, arch extending beyond level of prefemoral process; anterior bend moderately sharp and well defined, located at 1/3 length; peak long, about 1/2 acropodite length, flexed ventrad with apex at midlength; apical curve located at about 7/8 length, sharply bent at about 45° angle from peak, not forming arc; distal zone short, straight, angled slightly into arch, directed toward prefemoral process; tip acuminate and simple, not reflexed. Lamina of medial flange arising at base of anterior bend and continuing to apical curve, expanding basally into small, subrounded lobe representing flange then narrowing sharply at flexure. Tooth short, broadly rounded apically, located distal to flexure of peak but on lamina of medial flange, well separated from lobe of flange. Lateral flange displaced proximad, arising on distal extremity of peak, terminating near midlength of distal zone, broadly expanded into rounded lobe with irregular edge. Prostatic groove running along inner face of acropodite basally, crossing to lateral side at anterior bend and continuing to tip.

Male paratypes.— One male paratype has orange paranota and stripes rather than yellow. There is considerable gonopodal variation. All paratypes have apically bifurcate prefemoral processes, making the holotype the only male in the type series with a simple structure. The components are short, however, and the lateral one is generally slightly larger. Every projection of the acropodite also varies to some degree. The lobe representing the medial flange is much larger with a more rounded margin on one specimen, and the tooth of this individual is reduced and located closer to the lobe. On two paratypes the tooth is short and acuminate, rather than broadly rounded. The lateral flange is not expanded on one specimen, being long and narrow; on the others, however, it is clearly demarcated from the stem of the acropodite. The arch and overall curvature of the acropodite are constant.

Female paratype.— Length 38.8 mm, maximum width 9.0 mm, W/L ratio 23.2%, depth/width ratio 71.1%. Agreeing essentially with the holotype in somatic features except paranota more strongly depressed, creating appearance of more highly arched body.

Cyphopods *in situ* with side of receptacle visible, valves directed subdorsolaterad. Receptacle large, cupped around end of valves, extending completely around lateral side and halfway down medial, surface convoluted with deep folds and ridges. Valves with surface finely granulated.

Ecology.— The type specimens of *areolata* were collected slightly outside the cove environment typical of montane "sigmoid" xystodesmids. They were in standard climax deciduous forest on a hillside adjacent to a cove. In addition, they were under thick leaf layers on relatively soft substrate, rather than under thin layers on hard soil. Thus, *areolata* appears to inhabit a biotope similar to that occupied by *latior*.

Distribution.— Central Buncombe County, North Carolina (Fig. 132). The area lies southeast of Asheville in the vicinity of Busbee, the Butler Mountains, and Baldwin Gap, between US highways 25A and 74. Specimens were examined as follows:

NORTH CAROLINA: *Buncombe Co.*, 7.0 mi. SE Asheville, along co. rd. 3121 0.1 mi. W jct. co. rd. 3119, M, 5F, 8 September 1977 (NCSM A1714) and 4M, 3F, 9 September 1977

(NCSM A1716) TYPE LOCALITY; and 7.8 mi. SE Asheville, along co. rd. 3129, 0.9 mi. N jct. co. rd. 3128, F, 8 September 1977 (NCSM A1715).

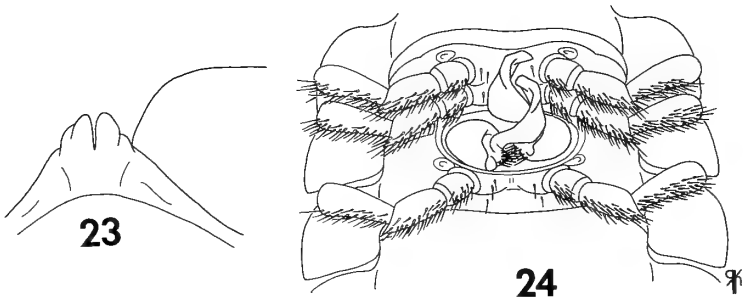
Remarks.— *Sigmoria areolata* is a highly localized endemic species known only from the area around Baldwin Gap in central Buncombe county. This area was revisited in June 1979, but no specimens were encountered.

Sigmoria areolata is a divergent member of the *latior* group and differs from the basic pattern in several particulars. It is the only species in which the peak is not long and narrow. The location of the tooth on the lamina of the medial flange is another unique feature of *areolata*. The yellow color pattern and preference for general hardwood forests instead of coves indicate a close relationship with *latior,* particularly *l. munda* with which it is sympatric. Aside from *latior, areolata* is the only montane "sigmoid" xystodesmid to shun coves for general forests. The condition of the tooth suggests an early stage in the evolution of separate laminas for the tooth and medial flange from an ancestor which lacked the former. Consequently, *areolata* may be a relict form which retained the primitive tooth-flange condition and developed specializations of its own.

Sigmoria stibarophalla, new species Figs. 23-28, 132-133

Type specimens.— Male holotype (NCSM A1720) and 3 male and 2 female paratypes collected by R.M. Shelley, 9 September 1977, from Buncombe Co., NC, 7.2 mi. ESE Fairview, along NC highway 9, 0.5 mi. N junction of county road 2801. Male and female paratypes deposited in FSCA and RLH.

Diagnosis.— A large species of *Sigmoria* with medial flange on proximal portion of peak and with red paranota and red transverse stripes along caudal margins of metaterga; gonopods with following diagnostic characters: prefemoral process small, cuneate, oriented parallel to peak of acropodite arch; acropodite thick and massive; basal zone with basal lobe on ventral surface; anterior bend sharp, well defined, located about 1/3 length; peak relatively flat and long, rising slightly distad, about 1/2 of acropodite length; apical curve very sharp, forming arc with very narrow diameter; distal zone short, tucked tightly under distal extremity of peak, visible only in lateral view, obscured by medial flange in medial view; tip reflexed; medial flange long and wide, arising at anterior bend, terminating at or beyond apical curve, obscuring all details of acropodite distal to anterior bend in medial view; tooth absent; lateral flange displaced proximad, beginning proximal to apical curve, terminating in narrow lamina extending length of distal zone to near tip.



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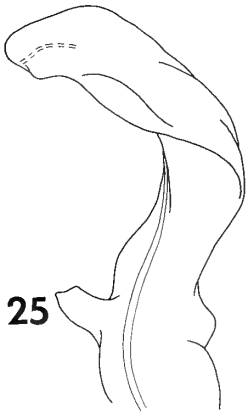

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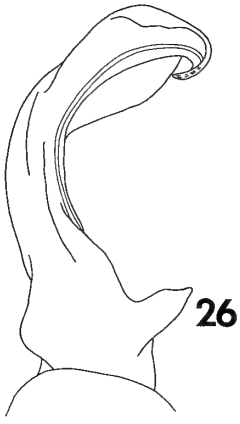

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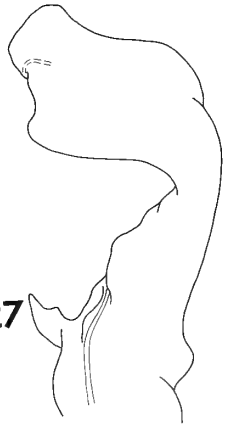

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Holotype.— Length 43.3 mm, maximum width 9.7 mm, W/L ratio 22.4%, depth/width ratio 61.9%. Segmental widths as follows:

collum	6.7 mm	6th-14th	9.7
2nd	8.0	15th	9.4
3rd	8.8	16th	9.0
4th	9.2	17th	7.8
5th	9.4	18th	6.0

Color in life: paranota red; metaterga black with wide, red, transverse stripes along caudal margins connecting paranotal spots; collum with red stripes along both anterior and caudal margins.

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 4.6 mm, interantennal isthmus 1.4 mm. Antennae reaching back nearly to caudal edge of third tergite, relative lengths of antennomeres 2>3>4=5>6>1>7. Facial setae as follows: epicranial and interantennal absent, frontal 1-1, genal 3-3, clypeal about 14-14, labral about 18-18, merging with clypeal series and continuing for short distance on genal border, about 2 setae on each side.

Dorsum moderately coriaceous. Collum very broad, extending beyond margins of following tergite. Caudolateral corners of paranota rounded on segments 1-6, becoming progressively more blunt and acute thereafter.

Process of 4th sternum (Fig. 23) much shorter than width of adjacent coxae; knobs and elevated areas of 5th sternum moderately distinct; sternum of segment 6 slightly recessed between 6th legs and deeply, convexly recessed between 7th to accommodate gonopodal acropodites, 7th legs set slightly farther apart than 6th. Postgonopodal sterna without lobes, with varying shallow impressions and grooves on segments 8-11 and one wide central impression on remaining segments.

Gonopodal aperture broadly rounded, 3.9 mm wide and 2.3 mm long at midpoint, indented slightly along anteriolateral edge, sides raised above metazonal surface. Gonopods *in situ* (Fig. 24, not this specimen) with right gonopod laying transversely in aperture, overlapping left gonopod at base of flange of latter, extending forward to between 7th legs; left gonopod extending essentially straight forward over 6th sternum to between 7th legs. Gonopod structure as follows (Figs. 25-26): prefemoral process short, cuneate, directed anteriad, subparallel to peak of arch. Acropodite thick and massive, arch extending beyond level of prefemoral process; basal zone with basal lobe on ventral surface; anterior bend sharp, well defined, located at about 1/3 length; peak flattened, slightly higher distally; apical curve very sharp, forming arc with very narrow diameter, located at 3/4 length; distal zone short, tucked tightly under distal extremity of peak, visible only in lateral view, obscured in medial view by medial flange; tip reflexed, directed toward underside of peak. Medial flange greatly enlarged, arising at anterior bend and terminating at apical curve, slight indentation at midlength, obscuring all details of acropodite distal to anterior bend in medial view. Tooth absent. Lateral flange displaced proximad, beginning as moderately wide lobe on distal extremity of peak, narrowing at apical curve and continuing to near tip. Prostatic groove running along inner surface of acropodite, crossing to lateral side at anterior bend and continuing to tip.

FIGS. 23-28, *Sigmoria stibarophalla.* 23, process of 4th sternum of holotype, caudal view. 24, gonopods *in situ,* ventral view of specimen from 6.5 mi. N Lake Lure (town), Rutherford Co., North Carolina. 25, telopodite of left gonopod of holotype, medial view. 26, the same, lateral view. 27, telopodite of left gonopod of specimen from same Rutherford Co. locality, medial view. 28, the same, lateral view. Scale line for fig. 24 = 1.00 mm; line for other figs. = 1.00 mm for each.

Male paratypes.— The male paratypes agree closely with the holotype in all particulars.

Female paratype.— Length 47.8 mm, maximum width 10.6 mm, W/L ratio 22.2%, depth/width ratio 71.7%. Agreeing with holotype in somatic features, with following exceptions: body noticeably narrower through about segment 8, widening thereafter to maximum width around segments 13-14, paranota slightly more depressed.

Cyphopods *in situ* with side of receptacle visible in aperture, valves oriented dorsoventrally in body, directed subcaudad. Receptacle large, hood-like, cupped over ventral end of valves, extending halfway down lateral and medial sides of valves, surface convoluted with deep ridges. Valves moderate, surface finely granulate.

Variation.— The prefemoral process is short and cuneate in all males, but a few possess an apical bifurcation. The process is reduced to a small, acuminate spur which barely projects from the prefemur in one male from Rutherford County (NCSM A2031). The length of the peak varies and extends only to the level of the prefemoral process in a few males rather than overhanging it as in the holotype. The length of the distal zone also varies and is longer in some individuals than in the holotype. In specimens from the eastern fringe of the range in Rutherford County (NCSM A1744, A2031), the medial flange is much wider and longer than in the holotype, extending beyond the apical curve onto the distal zone and the lateral side of the acropodite (Figs. 27-28).

Ecology.— *Sigmoria stibarophalla* is a cove dwelling species.

Distribution.— A small area in the eastern Blue Ridge Mountains of Buncombe County and adjacent parts of Henderson and McDowell counties, North Carolina (Fig. 132). The range extends down onto the Blue Ridge escarpment in western Rutherford County. Specimens were examined as follows:

NORTH CAROLINA: *Buncombe Co.,* 7.2 mi. ESE Fairview, along NC hwy. 9, 0.5 mi. N. jct. co. rd. 2801, 4M, 2F, 9 September 1977 (NCSM A1720) TYPE LOCALITY; 7.3 mi. SSE Fairview, along co. rd. 2801, 0.2 mi. E jct. NC hwy. 9, 2M, 9 September 1977 (NCSM A1722); 10.4 mi. E Fairview, along co. rd. 2791, 2.8 mi. E jct. NC hwy. 9, M, F, 9 September 1977 (NCSM A1717); N Bat Cave, M, F, 5 July 1955, collector unknown (RLH); and 9 mi. SE Black Mountain, along NC hwy. 9, 0.7 mi. N. jct. co. rd. 2801, M, 12 July 1976 (NCSM A993). *McDowell Co.,* 4.2 mi. S Old Fort, along co. rd. 1123, 0.7 mi. E jct. co. rd. 1103, 2M, 15 September 1977 (NCSM A1747); and 6 mi. S Old Fort, along co. rd. 1103, 0.4 mi. E Buncombe Co. line, 2M, 15 September 1977 (NCSM A1748). *Rutherford Co.,* 6.5 mi. N Lake Lure (town), along co. rd. 1314, 0.5 mi. W jct. co. rd. 1312, 3M, 3F, 14 September 1977 (NCSM A1744); and 4 mi. E Chimney Rock, along co. rd. 1306, 3.9 mi. N jct. US hwys. 64-74, M, F, 6 June 1978 (NCSM A2032).

Remarks.— *Sigmoria stibarophala* is a highly modified species of *Sigmoria* with several unique features. The thickness of the acropodite is exceeded only by that of *fumimontis,* and this condition plus the size of the medial flanges result in a different *in situ* gonopodal configuration for *stibarophalla.* There is insufficient space for both gonopods to lie

transversely in the aperture; thus, one extends forward over the 6th sternum to a greater distance than in any other species of the genus.

The two diagnostic features of *stibarophalla* are the enlarged medial flange and narrow apical curve. The former obscures everything else on the acropodite distal to the anterior bend in medial view, and the apical curve and distal zone are visible only in lateral view. The breadth of the medial flange varies, reaching a maximum in individuals from Rutherford County, where it extends onto the lateral side (Figs. 27-28). The apical curve is the narrowest in the genus; consequently, the distal zone of most specimens lies beneath and parallel to the distal extremity of the peak. In a few males the distal zone is directed towards the undersurface of the peak, so that the apical curve is nearly circular. Since the apical curve is so narrow and the distal zone does not extend dorsad or in the direction of the prefemur, *stibarophalla* is the only species of *Sigmoria* in which the prefemoral process is not directed toward a section of the acropodite. Here it projects anteriad and lies parallel to the peak.

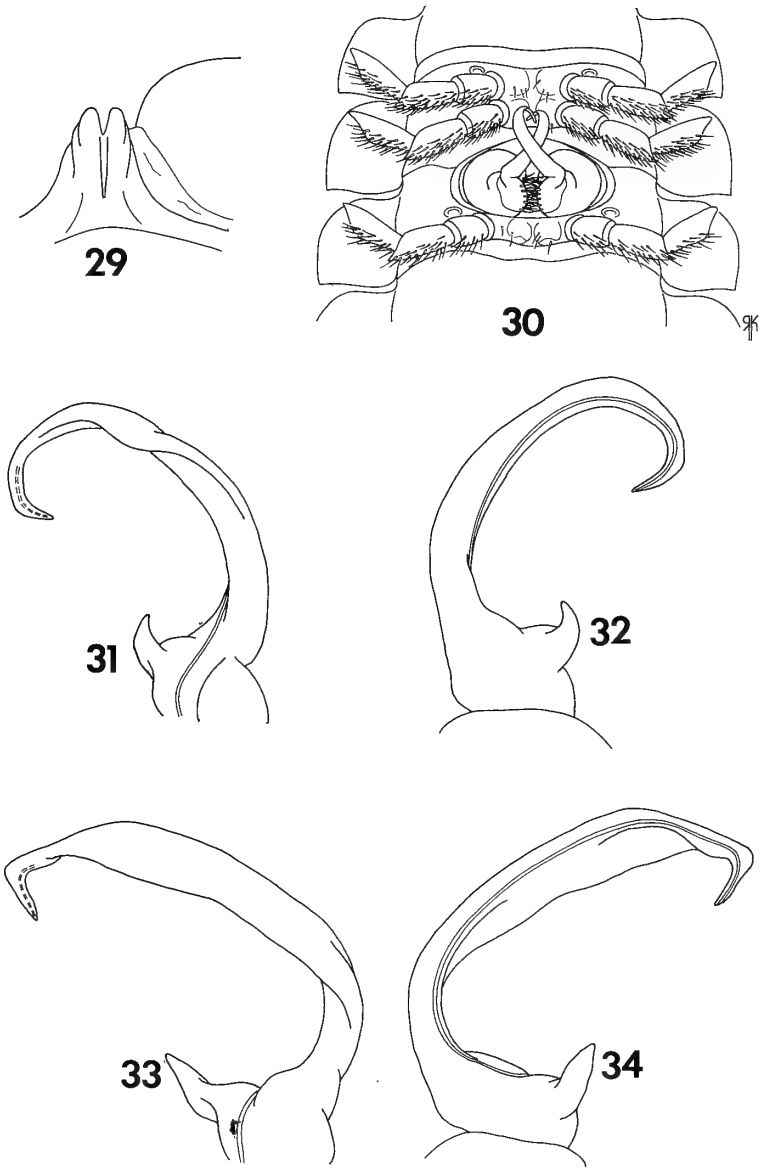
The unique features of *stibarophalla* make its affinities obscure, but I think it has enough features of the *latior* group to be placed here for now.

The *Simplex* Group

The *simplex* group consists of three localized species in the Toe River Valley and adjacent Blue Ridge Mountains of Yancey, Mitchell, and McDowell counties, North Carolina. Two of them, *truncata* and *sigirioides,* are the smallest in the genus, averaging less than 33 mm in length and 8 mm in width. The third species, *simplex,* is moderate in size, being generally subequal to *latior* in length but slightly narrower. The gonopods of these three species lack such specializations as the tooth, lateral flange, and reflexed tip, and are characterized by a short, wedge-shaped prefemoral process, a thin, relatively fragile acropodite, and a broad, poorly defined anterior bend. *Sigmoria truncata* and *sigirioides* have developed individual specializations to these primitive features, but *simplex* displays no real modifications. The existence of undiscovered species in the *simplex* group is more likely than in any other species group of *Sigmoria,* because of the remoteness of much of the area in western Mitchell and Yancey counties and adjacent Unicoi County, Tennessee. Field Collectors with enough time to explore the mountain valleys of this region on foot may be rewarded with the discovery of more representatives of this group.

Sigmoria simplex, new species Figs. 29-34, 132-133

Type specimens.— Male holotype (NCSM A668) and 4 male and 6 female paratypes collected by R.M. Shelley and J.C. Clamp, 24 July 1975,



FIGS. 29-34, *Sigmoria simplex*. 29, process of 4th sternum of holotype, caudal view. 30, gonopods *in situ*, ventral view of paratype. 31, telopodite of left gonopod of holotype, medial view. 32, the same, lateral view. 33, telopodite of left gonopod of specimen from 4.4 mi. SW Spruce Pine, Mitchell Co., North Carolina, medial view. 34, the same, lateral view. Scale line for fig. 30 = 1.00 mm; line for other figs. = 1.00 mm for 29, 31-32, 1.17 mm for 33-34.

from Mitchell Co., NC, 6.8 mi. SW Spruce Pine, along county road 1225, 0.6 mi. W junction of county road 1002, PNF. Male and female paratypes deposited in FSCA and RLH.

Diagnosis.— A moderate-size species of *Sigmoria* with medial flange on proximal portion of peak and with red or yellow paranota and concolorous stripes along caudal margins of metaterga; gonopods with following diagnostic characters: anterior bend poorly defined, beginning near base of acropodite and continuing smoothly to apical curve; peak broadly curved, apex at apical curve; apical curve varying from broadly continuous with anterior bend, to sharp and well defined; distal zone usually curved broadly into arc; tip simple, subacuminate, directed toward base of acropodite; medial flange relatively long and narrow, merging imperceptibly with stem of acropodite, with only slight to moderate lobe at midlength; tooth and lateral flange absent.

Holotype.— Length 38.5 mm, maximum width 8.5 mm, W/L ratio 21.8%, depth/width ratio 64.7%. Segmental widths as follows:

collum	6.4 mm	6th-14th	8.5
2nd	7.3	15th	8.2
3rd	7.7	16th	7.8
4th	8.3	17th	7.0
5th	8.4	18th	5.5

Color in life: paranota red, metaterga black with wide, red, transverse stripes along caudal edges connecting paranotal spots; collum with red stripes along both anterior and caudal edges.

Somatic features similar to those of *l. latior,* with following exceptions:

Width across genal apices 4.6 mm, interantennal isthmus 1.2 mm. Antennae reaching back to middle of third segment; relative lengths of antennomeres 2>3>6>4=5>1>7. Facial setae as follows: epicranial and interantennal absent, frontal 1-1, genal 2-2, clypeal about 10-10, labral about 12-12.

Collum broad, extending slightly beyond ends of following tergite. Caudal edges of all tergites relatively straight. Scapulorae pronounced.

Process of 4th (Fig. 29) and 5th sterna low and indistinct, much shorter than widths of adjacent coxae; 6th sternum slightly recessed between 7th legs to accommodate apical curvature of acropodites, 7th legs set slightly farther apart than 6th. Postgonopodal sterna without lobes, relatively flat, with shallow impressions and grooves.

Gonopodal aperture subelliptical, 3.2 mm wide and 1.7 mm long at midpoint, indented on anteriolateral margin, sides slightly elevated above metazonal surface, caudomedial edge raised into slight lobe. Gonopods *in situ* (Fig. 30, of paratype) with acropodites overlapping in midline and extending straight forward over anterior edge of aperture to between 7th legs, apices crossing. Gonopod structure as follows (Figs. 31-32): prefemoral process short, acuminate and simple, directed toward midlength of acropodite. Acropodite relatively thin, arch broad, overhanging and extending well beyond level of prefemoral process; anterior bend broad, poorly defined, beginning near base and continuing into peak region; latter broadly curved, apex distally at apical curve; apical curve broad but relatively well defined, subcontinuous with anterior bend through peak, beginning about 3/4 length, subtending semicircle; distal zone moderately long, curved broadly into arc; tip simple and subacuminate, directed

toward base of acropodite. Medial flange long, merging imperceptibly with stem of acropodite, arising near start of anterior bend, expanding rapidly near peak of arch into relatively small, rounded lobe, slightly obscuring stem of acropodite, narrowing rapidly distal to lobe and merging into stem of acropodite at beginning of apical curve. Tooth and lateral flange absent. Prostatic groove running along inner surface of acropodite, crossing from medial to lateral sides on basal zone and continuing to tip.

Male paratypes.— The male paratypes agree with the holotype in most features, but the prefemoral process is apically bifurcate on two specimens.

Female paratype.— Length 41.3 mm, maximum width 9.2 mm, W/L ratio 22.0%, depth/width ratio 72.5%. Agreeing with holotype in somatic features, but paranota much more strongly depressed, angling sharply ventrad, producing appearance of more highly arched body.

Cyphopods *in situ* with side of receptacle visible in aperture, valves directed caudolaterad. Receptacle moderate in size, extending slightly down lateral side of valves, surface wrinkled with numerous ridges. Valves large, surface wrinkled.

Variation.— The color of *simplex* varies, and about half the specimens I collected had yellow paranota and stripes rather than red. Both colors were represented in the material collected in Mitchell County, 4.4. mi. SW Spruce Pine (NCSM A1989). These color differences are not associated with anatomical changes. However, one male in this sample has epicranial setae in the amount of 1-1.

The length and height of the arc of the acropodite varies, along with the degree to which it overhangs the prefemoral process. In males from Crabtree Meadows the arc is short, high, and distally rounded, and the acropodites extend only slightly beyond the level of the prefemoral process. In other males, however, the arc is longer, lower, and flatter, and the acropodite extends well beyond the prefemoral process in medial view. The condition in the holotype is about halfway between these two extremes. The males in NCSM sample A1989 (Figs. 33-34) from 4.4 mi. SW Spruce Pine have the longest arc, and there is also an apical difference in that the tip is not bent inward into the arc but instead points downward toward the coxa in medial view. The apical curve is superimposed on the arc, which obscures most of it. Associated with the arc variation are differences in length and configuration of the medial flange. It tends to be longer and more uniform in width in specimens with longer arcs, and the rounded lobe at midlength is reduced. Hence, in the extreme case of sample A1989, the flange may be described as being long and narrow, poorly demarcated from the stem of the acropodite, arising on the anterior bend, expanding gradually to about midlength of the peak, then narrowing rapidly and merging with the stem of the acropodite at the apical curve, or about 3/4 length. It is difficult to determine exactly where the flanges of these males begin or end, because they do not expand into a definite rounded lobe as do those of the holotype.

There is no discernible geographic pattern to this gonopodal variation.

Ecology.— *Sigmoria simplex* is a cove dwelling species.

Distribution.— A small, rectangular area in the eastern Blue Ridge mountains around the common borders of Mitchell, Yancey, and McDowell counties, near the town of Little Switzerland (Fig. 132). It can be roughly described as bounded by US highway 19E on the northwest, and NC highways 22, 80, and 226A on the northeast, southwest, and southeast, respectively. Specimens were examined as follows:

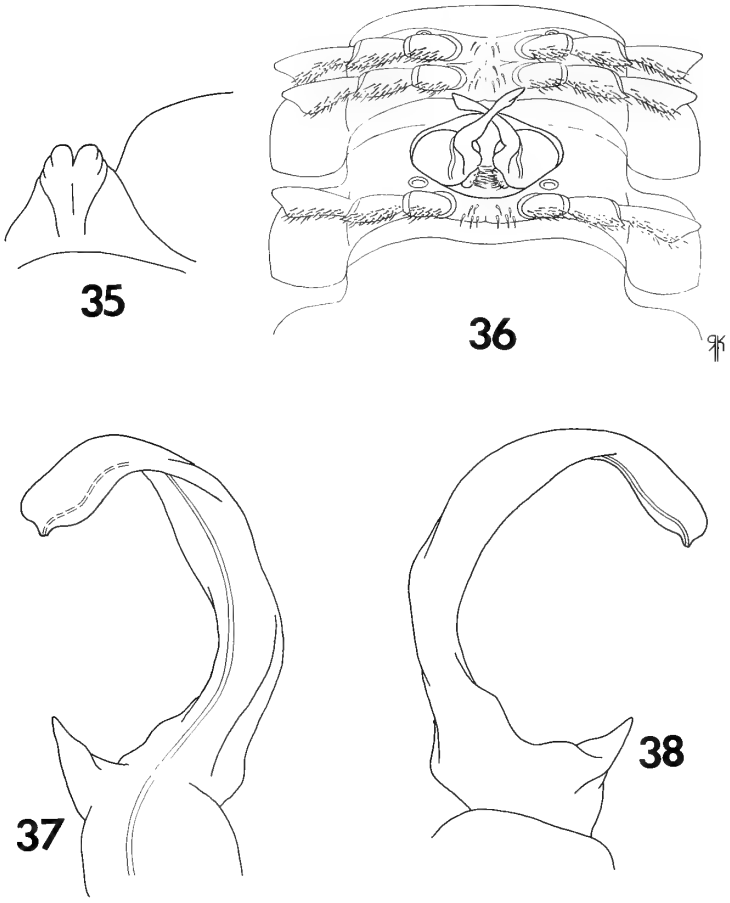
NORTH CAROLINA.— *Mitchell Co.,* 4.4 mi. SW Spruce Pine, along co. rd. 1002, 0.4 mi. S jct. US hwy. 19E, PNF, 8M, 9F, 21 May 1978 (NCSM A1989); 6.8 mi. SW Spruce Pine, along co. rd. 1225, 0.6 mi. W jct. co. rd. 1002, PNF, 5M, 6F, 24 July 1975 (NCSM A668) TYPE LOCALITY; 6.4 mi. SW Spruce Pine, along co. rd. 1002, 0.4 mi. S jct. co. rd. 1225, PNF, 5M, 3F, 24 July 1975 (NCSM A603); and 6.1 mi. SW Spruce Pine, along co. rd. 1002, 1.5 mi. S jct. co. rd. 1225, PNF, 2M, F, 24 July 1975 (NCSM A667). *Yancey Co.,* 2.4 mi. SE Celo, along co. rd. 1167, 0.5 mi. E jct. co. rd. 1171, PNF, 2M, F, 22 May 1978 (NCSM A1992); crawling on ground at Crabtree Meadows on Blue Ridge Pkwy., M, F, 19 July 1958, E.A. Chapin (NMNH); Crabtree Falls Recreation Area on Blue Ridge Pkwy., on hillside just W Falls, 6M, F, 3 August 1971, R.L. Hoffman and L.S. Knight (RLH); and Gooch Gap on Blue Ridge Pkwy, 3 mi. S Little Switzerland, PNF, M, 3 June 1974, R.L. Hoffman (RLH). *McDowell Co.,* Little Switzerland, along co. rd. 1420, 0.7 mi. W jct. NC hwy. 226A, PNF, 3M, F, 23 May 1978 (NCSM A2008).

Remarks.— *Sigmoria simplex* possesses the least specialized gonopod in the genus. The acropodite is a broadly curved, poorly defined arc, which lacks such specialized adornments as the sharp anterior bend, tooth, lateral flange, and reflexed tip. Even the medial flange is simple, being basically a long, narrow lamina which merges imperceptibly with the acropodite and has only a minimal lobe at midlength. Along with *latior, simplex* displays occasional yellow paranota and stripes, and bifurcation of the short prefemoral process. The following two species are close relatives of *simplex,* but have developed individual specializations of its primitive gonopod structure.

Sigmoria truncata, new species Figs. 35-38, 132-133

Type specimens.— Male holotype (NCSM A1987) and 3 male and 3 female paratypes collected by R.M. Shelley and W.B. Jones, 21 May 1978, from Mitchell Co., NC, 0.8 mi. S Bakersville, along NC highway 80, 0.7 mi. S junction with county road 1237, PNF. Five male and 7 female paratypes collected by R.L. Hoffman, 12 July 1962, from along NC highway 226, 3.0 mi. S Bakersville, PNF (RLH). Male and female paratypes deposited in FSCA.

Diagnosis.— A small species of *Sigmoria* with medial flange on proximal portion of peak and usually with red paranota and red stripes along caudal edges of metaterga, rarely with yellow markings; gonopods with following diagnostic characters: acropodite shortened, terminating in blunt tip immediately distal to flange; apical curve, distal zone, tooth, and lateral flange



FIGS. 35-38, *Sigmoria truncata.* 35, process of 4th sternum of holotype, caudal view. 36, gonopods *in situ,* ventral view of paratype. 37, telopodite of left gonopod of holotype, medial view. 38, the same, lateral view. Scale line for fig. 36 = 1.00 mm; line for other figs. = 1.00 mm for each.

absent; anterior bend poorly defined, a broad general curve leading into high, rounded arch; medial flange displaced distad, beginning near peak of arch; stem of acropodite widening in alternating perpendicular planes.

Holotype.— Length 34.4 mm, maximum width 7.3 mm, W/L ratio 21.2%, depth/width ratio 67.1%. Segmental widths as follows:

collum	5.6 mm	14th-15th	7.0
2nd	6.6	16th	6.5
3rd	6.9	17th	5.6
4th-13th	7.3	18th	4.7

Color in life: paranota red; metaterga black with wide, red, transverse stripes along caudal edges connecting paranotal spots; collum with red stripes along both anterior and caudal edges.

Somatic features similar to those of *I. latior,* with following exceptions:

Width across genal apices 4.2 mm, interantennal isthmus 1.4 mm. Epicranial suture faint and shallow. Antennae relatively short, reaching back only to caudal edge of second segment; relative lengths of antennomeres 2>3>4>5=6>1>7. Genae with distinct medial impressions. Facial setae as follows: epicranial and interantennal absent, frontal 1-1, genal 1-1, clypeal about 12-12, labral about 20-20, merging with clypeal series and continuing for short distance along genal border, about 4 setae on genal border on each side.

Collum broad, extending slightly beyond margins of following tergite. Paranota strongly depressed, continuing slope of dorsum and angling sharply ventrad; anterior corners rounded on all segments, posterior corners rounded through about segment 15. Peritremata distinguishable but moderately flat.

Process of 4th sternum (Fig. 35) much shorter than width of adjacent coxae; paramedial knobs between 4th legs and elevated areas between 5th legs (5th sternum) distinct; sternum of segment 6 moderately recessed between 7th legs to accommodate ends of acropodites, 7th legs set slightly farther apart than 6th. Postgonopodal sterna relatively flat, without lobes on caudal edges, with shallow transverse grooves originating between legs and deeper, wider, longitudinal grooves medially between caudal legs.

Gonopodal aperture elliptical, 2.7 mm wide and 1.4 mm long at midpoint, indented on anteriolateral margin, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 36, of paratype) with acropodites overlapping only at midlength, extending anteriolaterad to about level of aperture margin. Gonopod structure as follows (Figs. 37-38): prefemoral process short, acute, directed toward tip of acropodite. Acropodite widening in alternating perpendicular planes as follows: in medial view wide basally, narrower at beginning of anterior bend, widening again proximal to peak of arch and medial flange; arch extending only to about level of prefemoral process; anterior bend broad, poorly defined, beginning at about 1/4 length, continuing smoothly into peak of arch; peak high, rounded, arching downward to termination of acropodite; apical curve and distal zone absent; tip blunt, not reflexed, located at distal end of medial flange, directed toward prefemoral process. Medial flange displaced distad, beginning proximal to peak, curving bisinuately to tip. Tooth and lateral flange absent. Prostatic groove running along inner surface of acropodite to tip, distal portion obscured by flange.

Male paratypes.— The width of the stripe along the caudal edge of the metaterga varies in males of the type series, and is considerably narrower on some. The stripe even varies on a single individual, being relatively wide on the collum and segments 2-3, much narrower on segments 4-10, and much wider again on the remaining segments.

The paratypes agree essentially with the holotype in anatomical details. All are relatively small xystodesmids whose depressed paranota with rounded caudolateral corners impart a much more cylindrical appearance than is typical for the tribe Apheloriini.

The gonopods of the paratypes are little different from those of the holotype, except one individual lacks a darkened, sclerotized prefemoral process. There is a distinct rounded lobe at the location of the process, but the sclerotized acuminate point arising from this lobe is absent.

Female paratype.— Length 36.1 mm, maximum width 8.0 mm, W/L ratio 22.2%, depth/width ratio 70.0%. Anatomical details essentially the same as on the holotype, with the following exceptions: paranota more sharply depressed; collum not extending beyond ends of following tergite; sterna with large central impressions obscuring transverse grooves.

Cyphopods *in situ* with corner of valves and edge of receptacle visible in aperture; valves directed sublaterad. Receptacle relatively small and narrow, not overlapping ventral corner of

valves, extending slightly down lateral side of valves, surface convoluted with deep folds and ridges. Valves large, surface convoluted with folds.

Variation.— There is little variation among individuals of *truncata*. One male in sample A1993 from Yancey County displayed yellow paranota and stripes, but all other specimens were bright red. The only detectable anatomical variation involves the peak of the arch, which is flattened on some males. The arch in the holotype is higher and more rounded than in any other specimen.

Ecology.— Like most montane species of *Sigmoria, truncata* inhabits cool, moist rhododendron coves or similar habitats along stream bottoms. However, it seems to occupy a slightly different microhabitat in these environments in that it can live in rhododendron litter as well as that of associated hardwood species. In Yancey County (NCSM A1993) I collected it in loose piles of leaves in a dense rhododendron thicket.

Distribution.— A small area in the central Toe River Valley along the border of Yancey and Mitchell counties, North Carolina (Figs. 132-133). The triangle formed by NC highways 197 and 226, and US highway 19E, encompasses all known localities. Specimens were examined as follows:

NORTH CAROLINA: *Mitchell Co.*, 0.8 mi. S Bakersville, along NC hwy. 80, 0.7 mi. S jct. co. rd. 1237, PNF, 4M, 3F, 21 May 1978 (NCSM A1987) TYPE LOCALITY; 3 mi. S Bakersville, along NC hwy. 226, PNF, 5M, 7F, 12 July 1962, R.L. Hoffman (RLH); and 7.5 mi. NW Spruce Pine, along NC hwy. 80, 1.2 mi. N jct. co. rd. 1178, PNF, M, 3F, 21 June 1980 (NCSM A3328). *Yancey Co.*, S Red Hill in Mitchell Co., Toe River bluffs along NC hwy. 197, PNF, M, 12 July 1962, R.L. Hoffman (RLH); about 5 mi. NE Micaville, along NC hwy. 80, 2500′, PNF, M, F, 12 July 1962, R.L. Hoffman and L.S. Knight (RLH); and 3.2 mi. N Micaville, along co. rd. 1308, 0.4 mi. N jct. co. rd. 1311, PNF, 4M, 22 May 1978 (NCSM A1993).

Remarks.— The specific name refers to the truncated acropodite, which appears to have been sliced distal to the flange. Consequently, the distal characters of the *Sigmoria* gonopod, the apical curve and distal zone, are absent from *truncata*. Another unusual feature is that the medial flange is displaced distad, beginning closer to the peak of the arch and farther from the beginning of the anterior bend than in most congeners. This characteristic is more noticeable on the highly arched gonopods such as those of the holotype. A final oddity is the fact that the stem of the acropodite proximal to the flange is wide in alternately perpendicular planes, a feature also exhibited by some forms of *nigrimontis*. Thus, in medial view the acropodite is wide basally, narrows for a short distance at the beginning of the anterior bend, then widens again before the flange begins. At the point where it narrows in medial view, the acropodite is turned slightly so that the wide dimension is perpendicular to the angle of view. Likewise, where the acropodite is wide in medial view, it is narrow from the perpendicular perspective.

As with *stibarophalla,* the unique features of *truncata* caused problems in determining its systematic position. Although highly specialized, the gonopod does demonstrate three features diagnostic for *Sigmoria:* a short prefemoral process, long medial flange on the proximal portion of the peak, and a flattened peak, which is best illustrated by non-type males. The acropodite of *truncata* could be approximated by cutting that of the variant of *simplex* shown in Figs. 41-42 at the end of the medial flange, thus removing the apical curve and distal zone. The flange would be a little long for *truncata* and originate too close to the base of the acropodite, but the resemblance would be close nevertheless. Geographically, *truncata* occurs between *simplex* and *sigirioides,* both clear species of *Sigmoria,* and nearest the variant of *simplex* it most closely resembles. Consequently, *truncata* is a highly specialized species of *Sigmoria* that is closely related to *simplex.* Ecological factors may have been important in its speciation in view of the unique ability of *truncata* to tolerate rhododendron litter.

Sigmoria sigirioides, new species Figs. 39-42, 132-133

Type specimens.— Male holotype (NCSM A1996) and 1 male and 5 female paratypes collected by R.M. Shelley and W.B. Jones, 22 May 1978, from Yancey Co., NC, 7.6 mi. N Burnsville, along county road 1340, 0.5 mi. S junction of county road 1417, PNF. Female paratype deposited in FSCA.

Diagnosis.— A small species of *Sigmoria* with medial flange on proximal portion of peak and with red paranota and red stripes along caudal edges of metaterga; gonopods with following diagnostic characters: acropodite very thin and fragile, arch extending only to level of prefemoral process; anterior bend relatively broad, continuing smoothly into high, rounded peak; apical curve well defined; distal zone elongated, directed perpendicular to peak, not curved into arch; tip simple; medial flange beginning near peak, extending from surface of acropodite at about 45° angle to sharply acute point, returning abruptly proximal to apical curve; tooth and lateral flange absent.

Holotype.— Length 32.8 mm, maximum width 7.3 mm, W/L ratio 22.3%, depth/width ratio 65.6%. Segmental widths as follows:

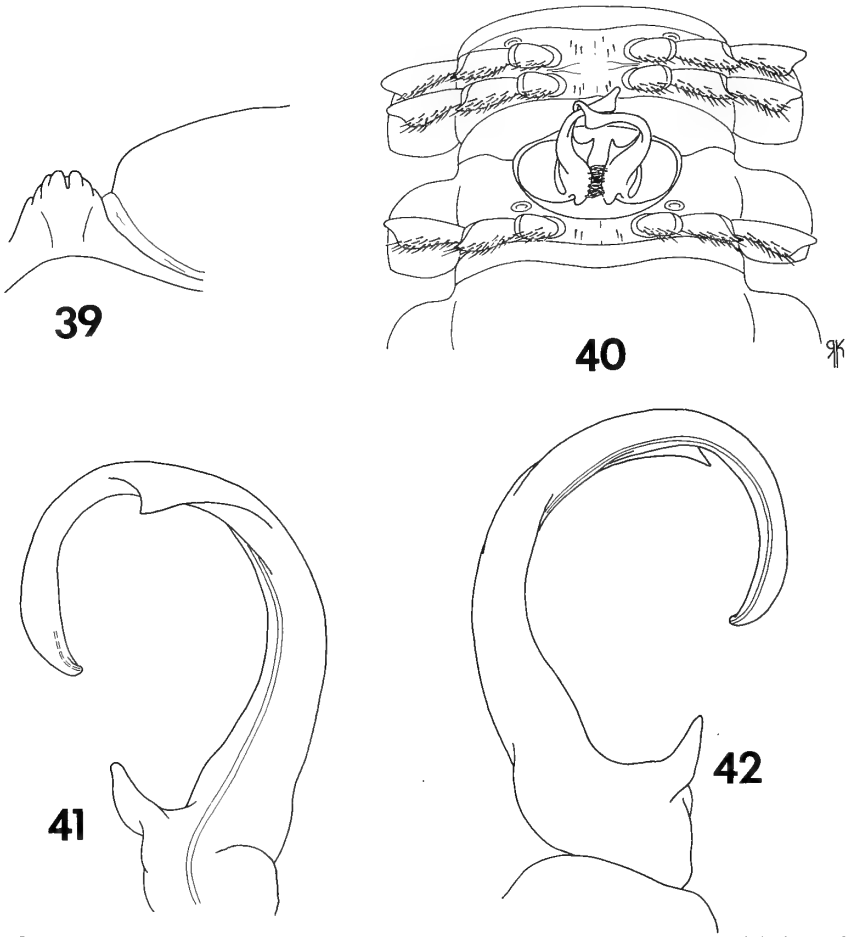
collum	5.6 mm	14th	7.0
2nd	6.5	15th	6.8
3rd	6.9	16th	6.5
4th-13th	7.3	17th	5.9
		18th	4.7

Color in life: paranota red; metaterga black with variable red stripes along caudal edges connecting paranotal spots, stripes narrow through segment 6, becoming gradually wider to segments 13-16, then narrowing slightly; collum with red stripes along both anterior and caudal edges.

Somatic features similar to *I. latior* with following exceptions:

Width across genal apices 4.0 mm, interantennal isthmus 1.4 mm. Antennae relatively long and slender, reaching back to middle of fourth segment, relative lengths of antennomeres 2>3>4>5=6>1>7. Genae with distinct medial impressions. Facial setae as follows: epicranial and interantennal absent, frontal 1-1, genal 2-2, clypeal about 13-13, labral about 14-14.

Collum moderate in size, extending slightly beyond ends of following tergite. Caudal margins of all tergites relatively straight. Paranota strongly depressed, angled sharply ventrad, caudolateral corners rounded through segment 6, blunt thereafter. Peritremata relatively faint, only slightly elevated above paranotal surface. Ozopores located near middle of paranota through segment 10, in caudal half thereafter.



FIGS. 39-42, *Sigmoria sigirioides*. 39, process of 4th sternum of holotype, caudal view. 40, gonopods *in situ*, ventral view of paratype. 41, telopodite of left gonopod of holotype, medial view. 42, the same, lateral view. Scale line for fig. 40 = 1.00 mm; line for other figs. = 1.00 mm for 39, 1.17 mm for 41-42.

Process of 4th sternum (Fig. 39) very small, much shorter than width of 3rd coxae; paramedial knobs and flattened areas of 5th sternum (between 4th and 5th legs) distinct, sharply set off from sternal surface; 6th sternum convexly recessed between 7th legs to accommodate telopodite, 7th legs set slightly farther apart than 6th. Postgonopodal sterna relatively flat, without lobes on caudal edges, with shallow transverse grooves originating between legs and wide central impressions obliterating transverse grooves on some segments.

Gonopodal aperture elliptical, 3.2 mm wide and 1.4 mm long at midpoint, indented on anteriolateral edge, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 40, of paratype) with acropodites overlapping either at midlength or with apical curve of one hooked over stem of other, in midline of aperture, extending forward slightly beyond anterior end of aperture. Gonopod structure as follows (Figs. 41-42): prefemoral process wedge shaped, tip rounded, directed toward tip of acropodite. Acropodite extremely thin and fragile, poorly sclerotized, arch high and rounded, extending only to level of prefemoral process; anterior bend broad, poorly defined, beginning about 1/4 length; peak relatively short and high, gently rounded; apical curve sharp, located at about 2/3 length; distal zone elongated, extending downward at about 90° from peak, not curved into arch; tip simple and rounded. Medial flange displaced distad, arising near end of anterior bend, angling sharply away from stem of acropodite at about 45° angle to sharply acute point, returning abruptly to acropodite stem proximal to apical curve. Tooth and lateral flange absent. Prostatic groove running along inner surface of acropodite proximal to anterior bend, crossing to lateral side near origin of flange and continuing to tip.

Male paratype.— The male paratype agrees with the holotype in all particulars, excepting that the medial flange is apically rounded rather than acuminate.

Female paratype.— Length 36.9 mm, maximum width 7.1 mm, W/L ratio 19.2%, depth/width ratio 83.1%. Agreeing closely with male in somatic features, with following exceptions: paranota more strongly depressed; caudolateral corners of midbody and posterior paranota more rounded; sterna very flat, generally without lobes or impressions.

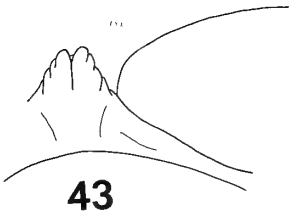
Cyphopods *in situ* with side of receptacle visible in aperture, valves directed dorsolaterad. Receptacle very large, extending completely down lateral side of valves and halfway down medial side, overlapping and partially obscuring end of valves, surface convoluted with deep ridges and folds. Valves moderate, surface with fine ridges.

Ecology.— *Sigmoria sigirioides* is a cove inhabiting species.

Distribution.— Known only from the type locality, which is about 1/2 mile from the Mitchell County line. The species probably occupies a small area in the Toe-Nolichucky River valley along the western border of Mitchell-Yancey counties, similar to that of *truncata* on the central border of these counties. The size of *sigirioides* coupled with the simple, non-reflexed tip and the absence of the tooth and lateral flange indicate affinity with simplex. However, the relationship does not seem to be as close as that between *simplex* and *truncata,* as evidenced by the similarity between the latter and the form of *simplex* 4.4 miles SW Spruce Pine.

The *Quadrata* Group

The *quadrata* group is characterized by a moderately long prefemoral process, a reduced medial flange, and the absence of such specializations as the tooth and reflexed tip. The tip, which is simple and blunt, projects in-



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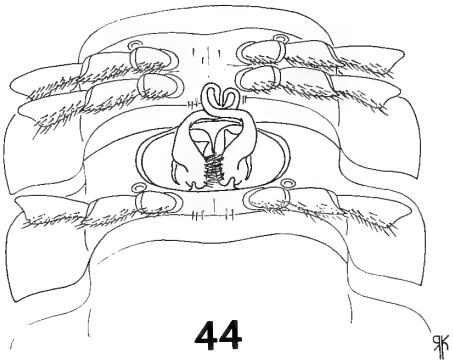

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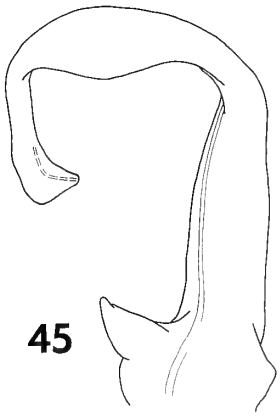

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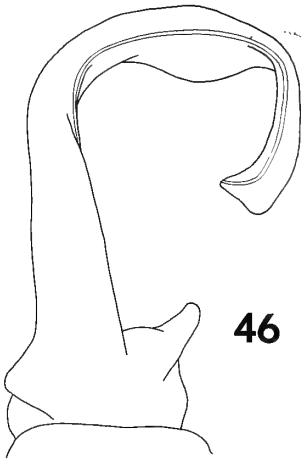

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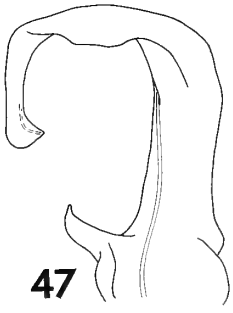

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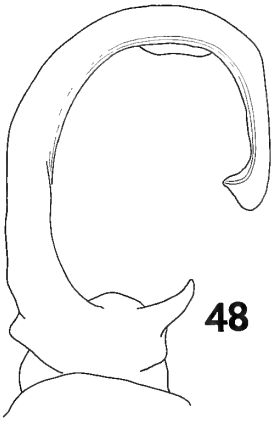

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ward into the arch at a distinct angle from the distal zone. *Sigmoria laticurvosa* possesses a lateral flange whereas *quadrata* lacks this structure. The millipeds are moderate in size and display red paranota and red metatergal stripes. The process of the 4th sternum is subequal in length to the width of the adjacent coxae, and the knobs between the 4th legs (5th sternum) are coalesced medially into a single projection. Species of the *quadrata* group occur south of Columbia in the fall zone region of the eastern Piedmont of South Carolina, between the Congaree and Savannah Rivers. They may once have occupied a larger area but have been reduced to the present range perhaps by inability to compete with the more adaptable *latior*. Thus, the *quadrata* group may be declining and headed toward extinction.

Sigmoria quadrata, new species Figs. 43-48, 137

Type specimens.— Male holotype (NCSM A2816) and 3 male and 1 female paratypes collected by R.M. Shelley and R.K. Tardell, 15 July 1979, from Lexington Co., SC, 4 mi. SW Lexington, along SC highway 604, 0.3 mi. S junction of SC highway 204, beside an unnamed creek. One male paratype deposited in FSCA.

Diagnosis.— A moderate-size species of *Sigmoria* with medial flange on proximal portion of peak and with red paranota and red transverse stripes along caudal margins of metaterga; gonopods with following diagnostic characters: acropodite moderately thick, arch subtending a square; basal zone with basal lobe on ventral surface; anterior bend and apical curve sharp, approximately 90°; peak of arch flattened; distal zone subequal in length to peak of arch; tip simple, bent sharply into arch; medial flange beginning at anterior bend, terminating at apical curve, moderately broad, widest section at peak of arch; tooth and lateral flange absent.

Holotype.— Length 40.4 mm, maximum width 9.9 mm, W/L ratio 24.5%, depth/width ratio 57.6%. Segmental widths as follows:

collum	6.6 mm	6th-13th	9.9
2nd	7.8	14th	9.5
3rd	8.2	15th	9.3
4th	9.0	16th	8.7
5th	9.5	17th	7.4
		18th	5.1

Color in life.— paranota red; metaterga black with wide, red transverse stripes along caudal edges connecting paranotal spots; collum with stripes along both anterior and caudal edges.

FIGS. 43-48, *Sigmoria quadrata.* 43, process of 4th sternum of holotype, caudal view. 44, gonopods *in situ,* ventral view of paratype. 45, telopodite of left gonopod of holotype, medial view. 46, the same, lateral view. 47, telopodite of left gonopod of specimen from 5.3 mi. NE Saluda, Saluda Co., South Carolina, medial view. 48, the same, lateral view. Scale line for fig. 44 = 1.00 mm; line for other figs. = 1.00 mm for 43 and 47; 1.17 mm for 45-46 and 48.

Somatic features similar to *I. latior,* with following exceptions:

Width across genal apices 4.3 mm, interantennal isthmus 1.6 mm. Antennae relatively long and slender, reaching back to just beyond caudal edge of 3rd tergite, relative lengths of antennomeres 2>3>4>6>5>1>7. Facial setae as follows: epicranial and interantennal absent, subantennal 1-1, frontal 1-1, genal 2-2, clypeal about 13-13, labral about 16-16, merging with clypeal series and continuing for short distance along genal border, about 5 setae on each side.

Paranota relatively flat, interrupting slope of dorsum. Collum broad, extending well beyond ends of following tergite. Caudolateral corners of paranota rounded through segment 6, becoming blunt and produced caudad posteriorly. Peritremata thick and conspicuous, strongly elevated above paranotal surface.

Process of 4th sternum (Fig. 43) large, apically acute, subequal in length to width of adjacent coxae; knobs between 4th legs coalesced medially into single process, shorter than width of adjacent coxae, flattened areas between 5th legs reduced and inconspicuous; 6th sternum slightly recessed between 7th legs. Postgonopodal sterna relatively flat, and varying shallow grooves and impressions. Coxae with low, rounded tubercles beginning on segment 8, becoming more sharply pointed caudally.

Gonopodal aperture subelliptical, 3.0 mm wide and 1.6 mm long at midpoint, indented along anteriolateral edges, sides flush with metazonal surface. Gonopods *in situ* (Fig. 44, of paratype) with acropodites overlapping at midlength in midline of aperture, extending forward to about anterior edge of aperture and curving dorsad toward body, tips overlapping. Gonopod structure as follows (Figs. 45-46): prefemoral process small, subtriangular. Acropodite moderately thick, well sclerotized, arch subtending a square, slightly overhanging prefemoral process; basal zone with basal lobe on ventral surface; anterior bend sharp, well defined, about 90°, located at about 1/3 length; peak flattened, about 1/3 of acropodite length; apical curve sharp, well defined, about 90°, located about 3/4 length; distal zone long, extending perpendicularly from peak; tip simple, projecting sharply inward into arch from distal zone, directed toward midlength of basal zone. Medial flange arising at anterior bend, terminating at apical curve, moderately broad with wide portion at midlength in region of peak. Tooth and lateral flange absent. Prostatic groove running along inner surface of acropodite basally, crossing to lateral side at anterior bend and continuing to tip.

Male paratypes.— The male paratypes agree essentially with the holotype.

Female paratype.— Length 38.1 mm, maximum width 9.1 mm, W/L ratio 23.9%, depth/width ratio 63.7%. Agreeing with holotype in somatic features except lacking subantennal setae and paranota slightly more depressed.

Cyphopods *in situ* with valves visible in aperture, receptacle situated internally against legs. Receptacle relatively small, situated anteriodorsad to valves, surface finely granulate. Valves moderate, surface finely granulate.

Variation.— There is little gonopodal variation in this species. The basal projection of the acropodite, which is never very large and only suggests a spine, is nearly absent from some individuals. On two males the apical curve forms a broad arc and the distal zone projects inward into the arch rather than downward toward the coxa. The prefemoral process is much longer and apically expanded on one male.

Ecology.— *Sigmoria quadrata* occurs under thin leaf layers on relatively hard substrates near rivers or creeks.

Distribution.— Fall zone region and eastern Piedmont Plateau of southern South Carolina, from the vicinity of Columbia to northern

Edgefield County (Fig. 137). Specimens were examined as follows:

SOUTH CAROLINA.— *Lexington Co.*, West Columbia, M, date and collector unknown (FSCA); 4 mi. SW Lexington, along SC hwy. 604, 0.3 mi. W jct. SC hwy. 204, at unnamed creek, 4M, F, 15 July 1979 (NCSM A2816) TYPE LOCALITY; and 4 mi. E Batesburg, along SC hwy. 602 at Hellhole Cr., M, 15 July 1979 (NCSM A2817). *Saluda Co.*, 5.3 mi. NE Saluda, along SC hwy. 39 0.9 mi. N jct. SC hwy. 450, M, F, 4 May 1977 (NCSM A1528); 6 mi. S Saluda, along SC hwy. 193, 0.1 mi. W jct. SC hwy. 119, 2M, 15 July 1979 (NCSM A2810); and 8 mi. NE Saluda, along US hwy. 378, M, 1958, N.B. Causey (FSCA). *Edgefield Co.*, 9.5 mi. N Edgefield, along SC hwy. 21, 0.2 mi. W jct. SC hwy. 403, at Little Stevens Cr., M, 15 July 1979 (NCSM A2819).

Remarks.— Both the anterior bend and apical curve of this species form sharp right angles, and the length of the distal zone is roughly equal to that of the peak. Since the tip of the acropodite is directed inward from the distal zone, the acropodite resembles a square in medial and lateral views, and hence the specific name, *quadrata*.

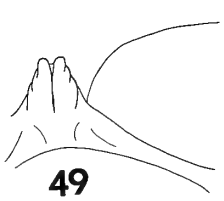
Sigmoria laticurvosa, new species Figs. 49-54, 137

Type specimens.— Male holotype (NCSM A2822) and 1 male and 1 female paratypes collected by R.M. Shelley and R.K. Tardell, 16 July 1979, from Aiken Co., South Carolina, 16 mi. NE Aiken, along SC highway 25 at McTier Cr. One male and 1 female paratypes collected by R.M. Shelley, 11 April 1978, from Aiken Co., 3.6 mi. NNW North Augusta, along SC highway 230, 0.1 mi. W junction of I-20. Male paratype deposited in FSCA.

Diagnosis.— A moderate-size species of *Sigmoria* with medial flange on proximal portion of peak and with red paranota and red transverse stripes along caudal margins of metaterga; gonopods with following diagnostic characters: acropodite moderately thick and heavy, arch broadly rounded, slightly overhanging prefemoral process; basal zone without lobe; anterior bend and apical curve poorly defined, united into single broad curve, continuous through peak; latter broadly rounded; distal zone moderately long, continuing broad curve of arch; tip simple, bent inward into arch from distal zone; medial flange short and narrow, obscuring at most only small section of acropodite stem; tooth absent; lateral flange present, moderately long and narrow.

Holotype.— Length 36.3 mm, maximum width 10.1 mm, W/L ratio 27.8%, depth/width ratio 57.4%. Segmental widths as follows:

collum	7.4 mm	6th-13th	10.1
2nd	8.0	14th	9.8
3rd	8.5	15th	9.4
4th	9.0	16th	8.7
5th	9.7	17th	7.7
		18th	4.4



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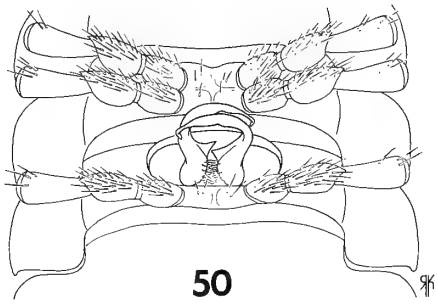

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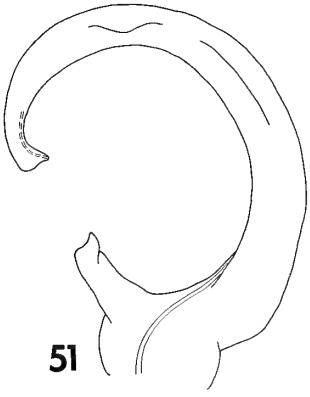

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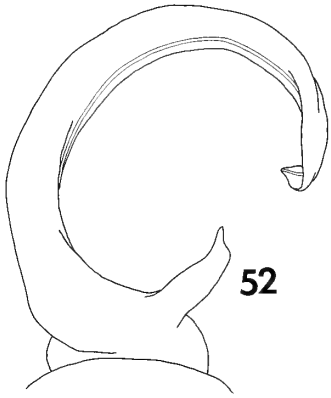

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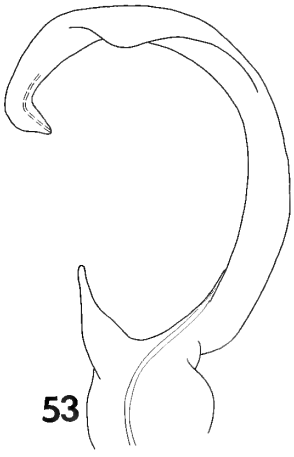

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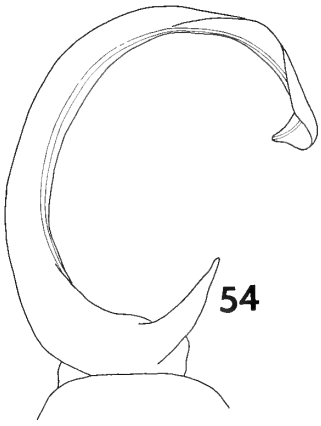

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Color in life.— paranota red; metaterga black with narrow, red, transverse stripes along caudal edges connecting paranotal spots; collum with stripes along both anterior and caudal edges.

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 4.4 mm, interantennal isthmus 1.6 mm. Antennae relatively long and slender, reaching back to just beyond caudal edge of 3rd tergite, relative lengths of antennomeres 2>3>4>5>6>1>7. Facial setae as follows: epicranial and interantennal absent, frontal 1-1, genal 3-3, clypeal about 14-14, labral about 20-20, merging with clypeal series and continuing for short distance along genal border, 2 setae on each side.

Paranota relatively flat, interrupting slope of dorsum. Collum broad, extending well beyond ends of following tergite. Caudolateral corners of paranota rounded on segments 1-5, becoming progressively more acute thereafter. Peritremata distinct, clearly demarcated from paranotal surface.

Process of 4th sternum (Fig. 49) large, subequal in length to width of adjacent coxae; knobs between 4th legs coalesced medially into single process, shorter than width of adjacent coxae, elevated areas between 5th legs reduced and inconspicuous; sternum of segment 6 only slightly recessed between 7th legs. Postgonopodal sterna generally flat and unmodified, with varying shallow grooves and impressions. Coxal tubercles beginning on 10th legs, becoming progressively longer and more acute caudally.

Gonopodal aperture broadly ovoid, 3.5 mm wide and 1.7 mm long at midpoint, indented on anteriolateral edge, sides flush with metazonal surface. Gonopods *in situ* (Fig. 50, of paratype) lying generally across opposite side of aperture in subparallel arrangement, tips overlapping anterior bend region of opposite acropodite. Gonopod structure as follows (Figs. 51-52): prefemoral process moderately long, bent mediad apically. Acropodite moderately thick and well sclerotized, arch a broad continuous curve slightly overhanging prefemoral process; anterior bend broad, poorly defined, beginning near base of acropodite, continuing smoothly through peak into apical curve; peak broadly rounded, apex at midlength; apical curve broad, poorly defined, continuous with anterior bend through peak, forming arc with broad diameter; distal zone moderately long, broadly curved; tip simple, bent inward into arch from distal zone, directed toward beginning of anterior bend. Medial flange very short and inconspicuous, located at peak of arch, arising from ridge on medial face beginning at anterior bend, not obscuring stem of acropodite. Tooth absent. Lateral flange long and narrow, beginning at midlength of distal zone, terminating proximal to tip. Prostatic groove crossing to lateral side of acropodite near base of anterior bend and continuing to tip.

Male paratypes.— The male paratype collected with the holotype agrees with the above description. The other male paratype (NCSM A1833), collected some 26.5 miles S of the type locality, varies slightly in several features (Figs. 53-54). Its prefemoral process is subequal in length to that of the holotype but is acuminate and not bent mediad apically. The arch of the acropodite is higher on this specimen, the peak is more flattened, and the distal zone is shorter. Finally, the medial flange is larger in every dimension, to where it overhangs and obscures a small section of the stem of the acropodite in medial view.

Female paratype.— Length 39.0 mm, maximum width 10.8 mm, W/L ratio 27.7%,

FIGS. 49-54, *Sigmoria laticurvosa.* 49, process of 4th sternum of holotype, caudal view. 50, gonopods *in situ,* ventral view of paratype. 51, telopodite of left gonopod of holotype, medial view. 52, the same, lateral view. 53, telopodite of left gonopod of specimen from 3.6 mi. NNW North Augusta, Aiken Co., South Carolina, medial view. 54, the same, lateral view. Scale line for fig. 50 = 1.00 mm; line for other figs. = 1.00 mm for 49, 1.17 mm for 51-54.

depth/width ratio 66.7%. Agreeing essentially with holotype in somatic features, except paranota more strongly depressed giving appearance of more highly arched body.

Cyphopods *in situ* with side of receptacle visible in aperture, valves directed dorsolaterad. Receptacle moderately large, hood-like, overlapping valves and extending down both sides, surface finely granulate. Valves small, surface finely granulate.

Ecology.— *Sigmoria laticurvosa* occurs under thin leaf layers on relatively hard substrates near rivers or creeks.

Distribution.— Known only from Aiken County, South Carolina (Fig. 137). Specimens were examined as follows:

SOUTH CAROLINA: *Aiken Co.*, no further locality data, M, 21 December 1957, W. Tarpley (FSCA); 16 mi. NE Aiken, along SC hwy. 25 at McTier Cr., 2M, F, 16 July 1979 (NCSM A2822) TYPE LOCALITY; and 3.6 mi. NNW North Augusta, along SC hwy. 230, 0.1 mi. W jct. I-20, M, F, 11 April 1978 (NCSM A1833).

Remarks.— The specific name of this milliped refers to the broad, smooth curve formed by the acropodite, which lacks the sharp apical curve and anterior bend, and the flattened peak of the arch, found in *quadrata*. For a time I thought *laticurvosa* might be a subspecies of the latter, but reproductive isolation of the two is indicated by differences in the prefemoral processes, curvatures of the acropodites, and medial and lateral flanges. However, the simple tips and almost identical processes of the 4th and 5th sterna indicate that they are more closely related to each other than to any other congener, and warrant formation of a species group.

The nearest known collecting localities of *laticurvosa* and *quadrata* are only about 10 miles apart, and the occurrence of two species, so similar anatomically, this close together in a topographically rather homogeneous area is most unusual. They appear to have arisen from a common ancestor and may once have been more allopatric than they currently are, which would have furthered speciation. Neither *quadrata* nor *laticurvosa* is particularly common. Thorough surveys of Saluda, Lexington, Edgefield, and Aiken counties have produced only five samples of the former and two of the latter, suggesting that they may be naturally declining and headed towards extinction. Preservation of hardwood communities along streambeds in these South Carolina counties is therefore advisable, to insure that man does not accelerate this process.

The *Stenogon* Group

The *stenogon* group contains two dissimilar species featuring relatively thin acropodites and relatively long prefemoral processes and peaks. *Sigmoria nantahalae* is the only species in the genus lacking a medial flange, and it is also characterized by a subrectangular tooth at about midlength of the peak and an abbreviated distal zone. *Sigmoria stenogon* is distinguished by a distal zone with two inward bends into the arch and a long, narrow

medial flange, extending beyond the beginning of the apical curve and terminating on the proximal portion of the distal zone. The color of both millipeds allows for accurate field identifications; *nantahalae* has red paranota and white stripes, while *stenogon* is violet in color. The *stenogon* group ranges from Henderson County, North Carolina, to the three northeasternmost counties of Georgia.

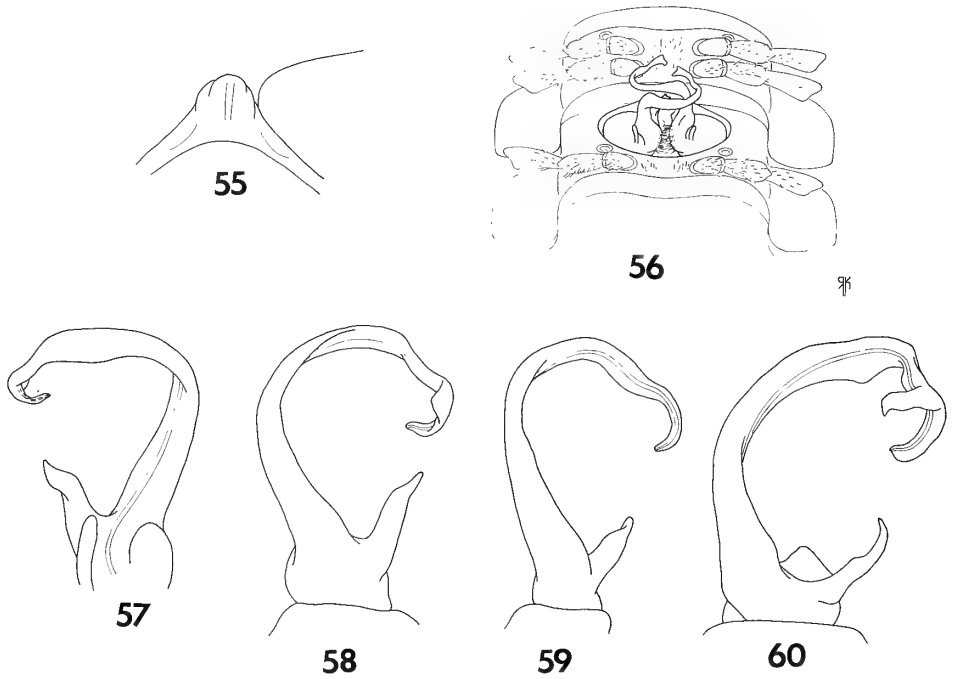
Sigmoria stenogon Chamberlin Figs. 55-60, 132-133

Sigmoria stenogon Chamberlin, 1942:5, pl. 2, fig. 12. Hoffman, 1950a:6-7. Chamberlin and Hoffman, 1958:51. Wray, 1967:152.

Type specimens.— Male holotype (RVC), female allotype, and 1 female paratype collected by M. Winslow, 21 July 1916, from Transylvania Co., NC, along "Bennett Gap Rd.," PNF. Bennett Gap is on the Haywood-Transylvania county line about 8.6 mi. NW Brevard, but there are no roads leading to the gap today, and there is no reason to believe that there was one in 1916. US highway 276 passes through Wagon Road Gap, a few miles north of Bennett Gap, and Forest Service Rd. #475 in western Transylvania County leads off this route and parallels the county line a few miles southeast of Wagon Road Gap. *Sigmoria stenogon* has never been collected in Haywood County, so the locality must be on the Transylvania side of the line. Since specimens have been taken from Pink Beds Recreation Area along Forest Service Rd. 475, it seems that the type locality was probably along the road to Wagon Road Gap (US hwy. 276) rather than one to Bennett Gap.

Diagnosis.— A moderate-size species of *Sigmoria* with medial flange on proximal portion of peak and with violet paranota and violet transverse stripes along caudal margins of metaterga; gonopods with following diagnostic characters: prefemoral process relatively long, thickness variable; acropodite thin and fragile, arch flattened and extending beyond level of prefemoral process; anterior bend sharp, well defined; peak long and flat; apical curve bisinuate, with two parts bending inward toward arch; tip reflexed; medial flange very long and narrow, scarcely wider than, and poorly demarcated from, stem of acropodite, arising at anterior bend, terminating at second inward bending part of apical curve; lateral flange variable but usually distinctly visible, when present ranging from subtriangular with margin broadly rounded to a long subrectangular projection arising perpendicularly from acropodite stem.

Holotype.— Length 38.9 mm, maximum width 8.9 mm, W/L ratio 23.0%, depth/width



FIGS. 55-60, *Sigmoria stenogon*. 55, process of 4th sternum of male from 5.7 mi. SE Brevard, Transylvania Co., North Carolina, caudal view. 56, gonopods *in situ*, ventral view of same specimen. 57, telopodite of left gonopod of holotype, medial view. 58, the same, lateral view. 59, telopodite of left gonopod of specimen from Flat Rock, Henderson Co., North Carolina, lateral view. 60, telopodite of left gonopod of specimen from 0.8 mi. SW Gerton, Henderson Co., lateral view. Scale line for fig. 56 = 1.00 mm; line for other figs. = 1.00 mm for 55, 0.75 mm for 57-58, 1.17 mm for 59-60.

ratio 65.2%. Segmental widths as follows:

collum	6.6 mm	7th-11th	8.9
2nd	7.0	12th	8.6
3rd	7.8	13th-14th	8.4
4th	8.2	15th	8.2
5th	8.4	16th	7.9
6th	8.7	17th	6.9
		18th	5.4

Color in life unknown; Chamberlin's comments (1942) were based on a preserved specimen that had been in alcohol for 36 years.

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 4.3 mm, interantennal isthmus 1.3 mm. Antennae short, extending back to just beyond caudal margin of 2nd tergite, relative lengths of antennomeres 2>3>5>6>4>1>7. Facial setae as follows: epicranial, interantennal, and genal absent; frontal 1-1, clypeal about 10-10, labral about 12-12.

Collum broad, extending well beyond ends of following tergite. Caudolateral corners of paranota rounded on segments 1-3, becoming progressively more acute thereafter. Peritremata slightly thickened.

Process of 4th sternum (Fig. 55) very small, much shorter than width of adjacent coxae; knobs between 4th legs and elevated flattened areas between 5th present but relatively small and inconspicuous; sternum of segment 6 not significantly depressed between 7th legs. Postgonopodal sterna generally flat, with shallow transverse grooves arising between legs. Coxae with low tubercles beginning on segment 8, becoming progressively longer and sharper caudally.

Gonopodal aperture broadly ovoid, 3.0 mm wide and 1.7 mm long at midpoint, indented along anteriolateral edge, sides flush with metazonal surface. *In situ* configuration of gonopods unknown, see comments under variation. Gonopod structure as follows (Figs. 57-58): prefemoral process moderately long, cuneate, subbisinuately curved, directed toward tip of acropodite. Acropodite thin and fragile, arch flattened and overhanging prefemoral process; anterior bend sharp and well defined, located at about 1/3 length; peak of arch flattened and long, about 1/3 of acropodite length; apical curve bisinuate, with broad inward bending proximal part followed by outward curving part then bending inward sharply again; distal zone relatively short, bent inward into arch; tip reflexed, directed toward midlength of basal zone. Medial flange very long and narrow, only slightly wider than, and poorly demarcated from, stem of acropodite, arising at anterior bend, terminating at beginning of second inward bending part of apical curve. Tooth absent. Lateral flange subtriangular, projecting from acropodite stem along second inward bending part of apical curve. Prostatic groove running along inner face of acropodite, crossing to lateral side at anterior bend and continuing to tip.

Female allotype.— Length 46.4 mm, maximum width 10.1 mm, W/L ratio 21.8%, depth/width ratio 70.3%. Agreeing with holotype in most somatic features, with following exceptions: paranota angled more sharply ventrad giving appearance of more highly arched body, corners rounded on segments 1-6; collum not extending beyond ends of following tergite; caudal margin of 2nd segment angled anteriad; peritermata lower and less distinct.

Cyphopods *in situ* with valves visible in aperture, receptacle located adjacent to legs. Receptacle subtriangular, situated dorsal to and not surrounding valves, surface finely granulate. Valves relatively large, surface finely granulate.

Variation.— *Sigmoria stenogon* displays the typical striped color pattern of other montane "sigmoid" xystodesmids but differs in having less of a

reddish tint to the paranota and stripes. The specimen I collected in Flat Rock, Henderson County (NCSM 2572) had purple stripes and paranota, whereas those from Bruce Falls in Transylvania County (NCSM A2054) were violet.

The *in situ* gonopodal configuration of the holotype is unknown, and the following description is taken from a male from Bruce Falls, Transylvania County (NCSM A2054) (Fig. 56). Each acropodite lies across the opposite side of the aperture and curves anteriad beyond the anterior edge of the aperture. The right one curves caudally behind the left, and the two do not actually overlap, although this could be accomplished with slight repositioning. The left acropodite extends farther anteriad over the 6th sternum than does the right, due to the more caudal position of the latter.

Several aspects of the gonopods vary, including the shape of the prefemoral processes, general curvatures of the acropodites, and configurations of the medial and lateral flanges. The prefemoral process is narrower and curved slightly at midlength in males from the northern part of the range near US highway 74 in Henderson County. In specimens from Hendersonville, Flat Rock, and Transylvania County, this process is thicker and similar to that of the holotype. The northern specimens exhibit a basal spur on the inner face of the acropodite just distal to the prefemur, but this spur is absent from the other males. The curvature of the acropodite varies, with the peak of the arch shorter and more curved in some individuals, resulting in less overhanging of the prefemoral process. The medial flange is always narrow but is more distinct and has a round apical lobe on the northern males. The lateral flange in Transylvania males resembles the condition in the holotype, but it varies greatly in specimens from Henderson County. The male from Flat Rock (Fig. 59) lacks the flange, whereas northern males (Fig. 60) possess a long, subrectangular projection. In these individuals the flange arises suddenly at a perpendicular angle from the acropodite, and in lateral view the gonopods appear almost chelate (Fig. 60). The margins of the flanges in these specimens are quite irregular, with several indentations and notches.

Ecology.— *Sigmoria stenogon* is a cove dwelling species.

Distribution.— Henderson and Transylvania counties, North Carolina, east of Pisgah Ridge and south of Hickorynut Gorge (Fig. 132). Specimens were examined as follows:

NORTH CAROLINA: *Transylvania Co.,* along "Bennett Gap Rd.," PNF, about 8.6 mi. NW Brevard, M, 2F, 21 July 1916, M. Winslow (RVC) TYPE LOCALITY; about 6 mi. N Brevard, Pink Beds Recreation Area, along US Forest Service Rd. #475, PNF, 2M, F, 13 July 1962, R.L. Hoffman (RLH); and 5.7 mi. SE Brevard, along co. rd. 1536, 1.8 mi. N jct. co. rd. 1591 at Bruce Falls, 3M, 9 June 1978 (NCSM A2054). *Henderson Co.,* Hendersonville, M, F, 11 August 1954, M.J. Westfall (RLH); Flat Rock, M, 18 October 1974, R.M. Shelley (NCSM

2572); 7.6 mi. NE Hendersonville, along co. rd. 1565, jct. co. rd. 1573, 2M, 2F, 12 July 1976 (NCSM A996); 8.8 mi. NE Hendersonville, along co. rd. 1719, 2.0 mi. N jct. co. rd. 1722, F, 13 September 1977 (NCSM A1740); 5.4 mi. N Hendersonville, along co. rd. 1528, 2.6 mi. N jct. co. rd. 1617, M, F, 13 September 1977 (NCSM A1736); and 0.8 mi. SW Gerton, along co. rd. 1594, 0.9 mi. SW jct. US hwy. 74, M, F, 13 September 1977 (NCSM A1738).

Remarks.— Chamberlin (1942) noted the "exceptionally narrow" gonopods of *stenogon,* but this is not a diagnostic character, as *sigirioides* and some specimens of *stenoloba* have gonopods that could fit this description. The chief diagnostic feature of *stenogon* is the bisinuate apical curve, which is unique to the species. Other traits which characterize the milliped include the large lateral flange of most individuals and the extremely narrow medial flange. As mentioned under variation, the lack of red pigment in the color of *stenogon* results in an unusual violet to purple hue to the paranota and stripes, a condition also displayed by *disjuncta.*

Sigmoria stenogon is not obviously related to any congener, so its systematic position has been a source of confusion. However, the thin acropodite suggests affinity with *nantahalae,* and the narrow and long medial flange, and reflexed tip, suggest relationship to the *latior* group. For the sake of convenience I combine *stenogon* and *nantahalae* into a species group, based mainly on their geographic proximity and thin acropodites.

Sigmoria nantahalae Hoffman Figs. 61-65, 132-133, 136, 138

Sigmoria nantahalae Hoffman, 1958:281-284, figs. 1-4. Wray, 1967:152.

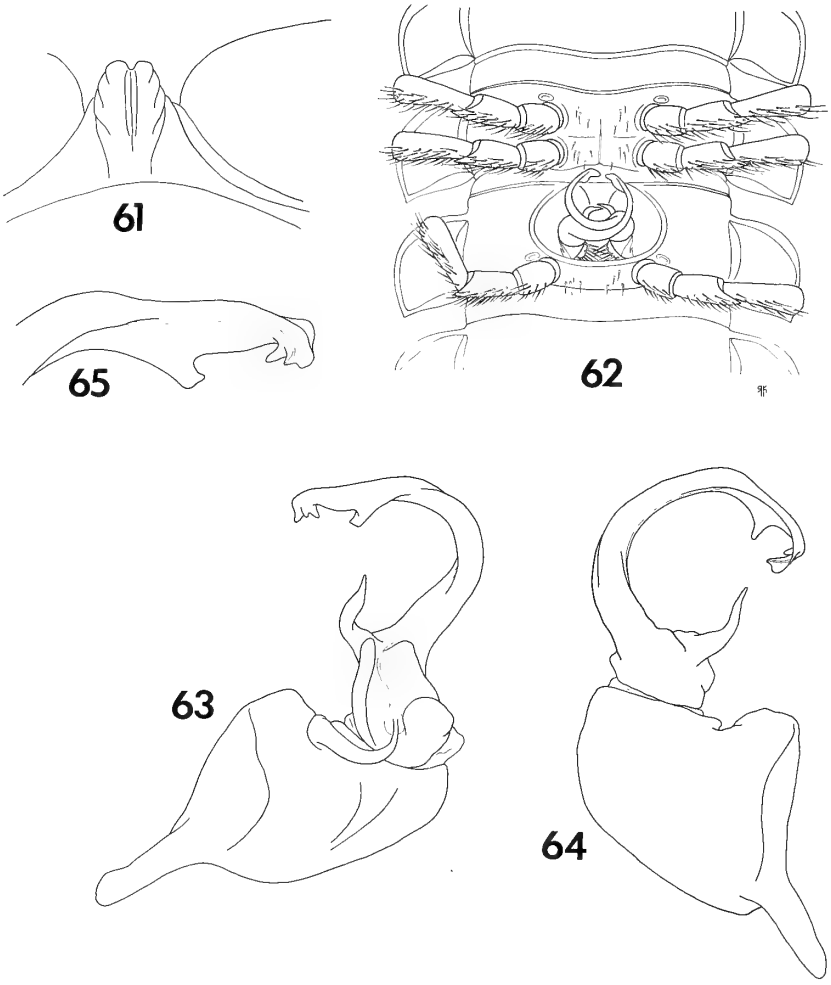
Type specimens.— Male holotype and male and female paratypes (NMNH 2460) collected by L. Hubricht, 6 May 1951, from Swain Co., NC, in Nantahala Gorge, along US highway 19, approximately 3 mi. NE Nantahala and 12 mi. SW Bryson City. Male and female paratypes in RLH.

Diagnosis.— A moderate-size species of *Sigmoria* without medial flange and with red paranota and white transverse stripes along caudal margins of metaterga; gonopods with following diagnostic characters: prefemoral process moderately long, acuminate, bent ventrad at midlength; acropodite relatively thin and fragile; anterior bend and apical curve well defined, latter about 90°; peak long and flattened; distal zone very short, with rounded lobe proximally in corner of apical curve; tip slightly reflexed, directed toward coxa; medial flange absent; tooth present but modified, subrectangular, located distal to midlength of peak, tapering into narrow distal flange terminating at apical curve; lateral flange present, long and moderately narrow.

Holotype.— The following observations are supplemental to the more complete description by Hoffman (1958).

Length 39.0 mm, maximum width 9.3 mm, W/L ratio 23.8%, depth/width ratio 62.0%. Segmental widths as follows:

collum	6.8 mm	15th	8.9
2nd	7.8	16th	8.2
3rd	8.3	17th	7.1
4th	8.8	18th	5.2
5th-14th	9.1		



FIGS. 61-65, *Sigmoria nantahalae*. 61, process of 4th sternum of holotype, caudal view. 62, gonopods *in situ*, ventral view of specimen from 5.9 mi. S Bryson City, Swain Co., North Carolina. 63, left gonopod of holotype, medial view. 64, the same, lateral view. 65, distal end of acropodite of same, subdorsal view. Scale line for fig. 62 = 1.00 mm; line for other figs. = 1.20 mm for 61, 1.00 mm for 63-64, and 2.00 mm for 65.

Color in life (Hoffman 1958): paranota bright vermillion; metaterga glossy black,with wide, light pearl gray stripes along caudal edges connecting paranotal spots; collum with gray stripe along caudal edge and vermillion stripe along anterior margin.

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 5.0 mm, interantennal isthmus 1.3 mm. Antennae reaching back to caudal edge of 3rd tergite, relative lengths of antennomeres 2>3>4>5>6>1>7. Facial setae as follows: epicranial, interantennal, frontal, and genal not detected, clypeal about 9-9, labral about 12-12.

Dorsum smooth, polished, becoming coriaceous on paranota. Collum moderately broad, ends not extending beyond those of following tergite. Paranota mildly depressed, continuing slope of dorsum, caudolateral corners rounded through segment 10, becoming blunt and progressively more acute posteriorly.

Process of 4th sternum (Fig. 61) small, shorter than widths of adjacent coxae; processes of 5th sternum distinct but much shorter than widths of adjacent coxae; 6th sternum convexly recessed between 7th legs to accommodate apical curvatures of acropodites. Postgonopodal sterna glabrous and flattened, without lobes on caudal edges, with narrow transverse grooves arising between leg pairs and wide, shallow, central impressions. Low, blunt coxal tubercles on legs of segments 8-16, slightly sharper on segments 10-14.

Gonopodal aperture broadly ovoid, 3.1 mm wide and 1.9 mm long at midpoint, indented on anteriolateral edge, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 62, not this specimen) with acropodites extending over opposite side of aperture, lying curved one inside other in midline, overlapping at about 2/3 length of region of peaks, extending forward slightly beyond anterior margin of aperture. Gonopod structure as follows (Figs. 63-64): prefemoral process moderately long, apically acute, bent ventrad at midlength; prefemur with lobe in midline of medial surface. Acropodite relatively thin and fragile, curvature overhanging and extending well beyond level of prefemoral process; basal zone with basal lobe on ventral surface; anterior bend relatively sharp, located at about 1/3 length; peak relatively long and flattened in medial view, apex on proximal part, nearly 1/2 of acropodite length; apical curve very sharp and well defined, about 90°, located at about 5/6 length; distal zone very short, no more than 1/6 of acropodite length, only slightly longer than tooth, with rounded lobe proximally in corner of apical curve, extending onto distal extremity of peak; tip expanded, slightly reflexed, directed toward coxa. Medial flange absent. Tooth present, located near midlength of peak, subrectangular, distal corner slightly produced, with narrow flange on distal side merging with stem of acropodite at apical curve. Lateral flange long and narrow, arising near midlength of peak at level of tooth, terminating proximal to tip. Prostatic groove arising in pit on prefemur, running along inner surface of acropodite basally, crossing to lateral side at anterior bend, opening terminally on reflexed tip.

Male paratypes.— The male paratypes agree with the above description in most structural details, except that they have the following facial setae missing from the holotype: frontal 1-1, genal 3-3.

Female paratype.— Length 42.6 mm, maximum width 9.4 mm, W/L ratio 22.1%, depth/width ratio 69.1%. Agreeing closely with males in somatic features, except paranota more strongly depressed, creating appearance of more highly arched body.

Cyphopods *in situ* with ends of valves and edge of receptacle visible in aperture, valves directed sublaterad. Cyphopod structure as described and illustrated by Hoffman (1958, fig. 4).

Variation.— The size of *nantahalae* varies, with some individuals of both sexes being quite large and bulky. Specimens from Nantahala Gorge are

among the smallest collected, while the largest are from Clay County, North Carolina, near Standing Indian Mountain (NCSM 2380).

On the gonopods the configuration of the prefemoral process and tooth vary, with the latter smaller than in the holotype in a few males. The length of the distal zone also varies, being only a short spur of the peak in a couple of specimens. The condition in the holotype is characteristic of most individuals.

Ecology.— Although *nantahalae* is primarily a cove inhabiting milliped, it can occupy other habitats and seems to be ecologically plastic. I have found it in places that were quite dry and open, with little shade to offset sunlight. In these sites *nantahalae* seeks refuge in matted leaf piles, where it is usually found in muddy leaves at the bottom of the pile. No other apheloriine species can burrow into these thick mats as well as *nantahalae,* and this behavioral adaptation to arid environments may partially account for its larger range. The larger individuals that I have collected were from these sites and found in leaf piles. In cove environments individuals seem to be smaller and occur under thin layers of leaves of hardwood species on relatively hard substrates near water sources.

Distribution.— Hoffman (1958) reported that *nantahalae* occurred in extreme western North Carolina and adjacent north Georgia, mainly in mountains surrounding the headwaters of the Nantahala and Hiwassee Rivers. It was known from the Nantahala, Cowee, and Valley River Mountains of North Carolina and the Blue Ridge of north Georgia, and he suggested that it would also be found in the Snowbird and Cheoah Ranges and the eastward extension of the Cowee Range near Cashiers, North Carolina, in southern Jackson County. Part of this prediction has come true, as *nantahalae* is common in the Cheoah and Snowbird Ranges in Graham County, North Carolina, but it has not been collected near Cashiers. The southernmost record from Jackson County is about 7 miles SW Cullowhee and some 10 miles N Cashiers. I believe that these individuals represent the range periphery in Jackson County. Moreover, I have seen no specimens from the Valley River Mountains (northern Clay and northeastern Cherokee counties, North Carolina) and have collected none there myself. The species is common on the northern slope of the Snowbird Mountains in Graham County, North Carolina, but it seems to be absent from the southern slope in Cherokee County, as I have made three trips to this area without finding the milliped. In fact, *nantahalae* has never been collected from Cherokee County, not even from the vicinity of Topton in the extreme northeastern corner, only a few miles from sites in Macon County where it has been found. It also appears to be absent from eastern Monroe County, Tennessee, which is not far from Joyce Kilmer Forest in Graham County,

North Carolina, where the milliped is common. I have thoroughly sampled the CNF in this area without finding the diplopod.

In summary, *nantahalae* ranges from Central Swain County, North Carolina, to southern Union County, Georgia, in mountains around headwater areas of the Hiwassee and Little Tennessee Rivers (Figs. 132-133). The northernmost record is from the Forney Creek area of the GSMNP, some 12 miles NW Bryson City; this record is the first from north of the Little Tennessee River and the GSMNP. Longitudinally, *nantahalae* ranges east-west from central Jackson to western Graham counties, North Carolina. It is strictly a montane species and is absent from the low, open valleys of central-western Clay and central-southern Cherokee counties, North Carolina. The only locality which does not fit this generalized description is that from Rabun County, Georgia, which is in the Savannah (Tallulah) River drainage. However, 13.3 miles W. Clayton is very near the Towns county line, which is the drainage divide between the Savannah and Hiwassee basins. Thus, it seems possible that the sample was unknowingly collected across the line in Towns County. Although it has never been collected there, *nantahalae* must occur in northwestern Rabun County, as this area is in the Little Tennessee drainage. Thus, the range of *nantahalae* is the third largest in *Sigmoria,* exceeded only by those of *latior* and *rubromarginata.* Specimens were examined as follows:

NORTH CAROLINA: *Swain Co.,* along Forney Creek in GSMNP, ca. 12 mi. NW Bryson City and 8.0 mi. W Park entrance, F, 9 May 1980 (NCSM A3018); 5.9 mi. S. Bryson City, along co. rd. 1140, 0.4 mi. S 1st bridge on co. rd. 1141, 4M, 2F, 16 May 1978 (NCSM A1908); 5.3 mi. SW Bryson City, along co. rd. 1309, 0.1 mi. W jct. co. rd. 1308, 2M, 16 May 1978 (NCSM A1909); 8 mi. SW Bryson City, no further locality data, F, 6 May 1951, L. Hubricht (RLH); ca. 12 mi. SW Bryson City, along US hwy. 19 in Nantahala Gorge, about 3 mi. NE Nantahala, 2M, F, 6 May 1951, L. Hubricht (NMNH 2460), M, F, 6 May 1951, L. Hubricht (RLH), and 5M, F, 18 August 1976 (NCSM A1359) TYPE LOCALITY; Nantahala, base of Cliff Ridge, M, 6 May 1951, L. Hubricht (RLH); and 1 mi. SW Nantahala, along US hwy. 19, 1.1 mi. NE Macon co. line, 2M, 24 June 1978, A.L. Braswell (NCSM A2148). *Graham Co.,* ca. 4.0 mi. E Fontana Village, along US For. Serv. rd. 520 to Cove Cr. Rec. Area on Fontana Lake, 0.1 mi. N jct. NC hwy. 28 and 3.7 mi. E jct. co. rd. 1245 to Fontana Dam, M, 16 May 1978 (NCSM A1913); Fontana Village, M, F, 16 May 1978 (NCSM A1918); Joyce Kilmer Memorial Forest, M, F, 20 May 1970, W.A. Shear (WAS) and 2M, F, 25 July 1974 (NCSM 2477); and 2.8 mi. WSW Robbinsville, along co. rd. 1127, 0.2 mi. W jct. co. rd. 1116, M, 25 July 1974 (NCSM 2476). *Jackson Co.,* 1.5 mi. S Speedwell, along Cullowhee Mtn. Rd., M, 25 October 1969, F.A. Coyle (WAS); 2.5 mi. SW Cullowhee, along Long Branch Cr., M, 17 July 1970, F.A. Coyle (NCSM A2104); 5 mi. SW Cullowhee, Wolf Cr. Biol. Preserve, M, F, 28 April 1976, H.W. Levi (NCSM A787) and M, 27 June 1977, J.A. Beatty (JAB); and 7 mi. S Cullowhee, along NC hwy. 107, 2F, 27 June 1977, J.A. Beatty (JAB). *Macon Co.,* Cullowhee Gap, M, 10 July 1958, R.L. Hoffman (RLH); 5 mi. NW Franklin, Shuler's Mine on Cowee Cr., 3M, 22 July 1961, R.L. Hoffman (RLH); Wesser Bald, F, 22 July 1949, R.L. Hoffman (RLH); 8.8 mi. NE Franklin, along US hwy. 23, 2M, 4F, 23 June 1950, L. Hubricht (RLH); 6.5 mi. W Franklin, along co. rd. 1310, 1.0 mi. E jct. US For. Serv. Rd. 711, M, 24 June 1978, A.L. Braswell (NCSM A2152); along co. rd. 1310 W Franklin, M, 29 June 1951, R.L. Hum-

phries (RLH); ca. 14 mi. SW Franklin and 5 mi. NW Rainbow Springs, along US For. Serv. rd. 437, M, 2 June 1977, A.L. Braswell (NCSM A1590); 5 mi. NW Highlands, along Buck Cr. Rd., 2M, 19 July 1961, R.L. Hoffman (RLH); 3.5 mi. N Highlands, M, F, 3 August 1958, R.L. Hoffman (RLH); and Coweeta Hydrological Station, 2.4 mi. W Otto, M, 1 August 1958, R.L. Hoffman (RLH); 2M, 8 June 1973, R.L. Duffield (RLH), and 3M, F, 6 July 1978 (NCSM A2327). *Clay Co.,* Tuni Gap at Macon Co. line, 10.2 mi. NE Hayesville, M, 20 July 1952, T. Howell (RLH); 5 mi. NE Shooting Creek, along US For. Serv. rd. M, F, 29 July 1974 (NCSM 2380); 4 mi. NE Shooting Creek, along US hwy. 64 at Glade Gap, 3673′, M, 20 July 1952, T. Howell (RLH); 2 mi. NE Shooting Creek, along US hwy. 64, 4 mi. W Glade Gap, M, 18 June 1954, J.T. Darlington (RLH); Shooting Creek vicinity, 4M, 5 June 1952, R.L. Hoffman (RLH); and 8.8 mi. NE Hayesville, along co. rd. 1311, 3F, 30 July 1974 (NCSM 2398).

GEORGIA: ?*Rabun Co.,* 13.3 mi. W Clayton, along US hwy. 76, 3M, 18 July 1961, R.E. Gordon (RLH). *Towns Co.,* 6.5 mi. SSW Hiawassee, Etona Glade Picnic Area along GA hwy. 66, ca. 1.0 mi. E jct. GA hwy. 180 E Brasstown Bald, M, 7 June 1953, L. Hubricht (RLH). *Union Co.,* 13 mi. SW Blairsville, along GA hwy. 60, 1.6 mi. W jct. GA hwy. 180, M, 9 July 1978 (NCSM A2349); 13.5 mi. SW Blairsville, 3 mi. S Gaddistown along creek, M, 3F, 4 July 1973, R.L. Hoffman (RLH); and 9 mi. SE Blairsville, along GA hwy. 180, 3.6 mi. E jct. US hwy. 19, Sosebee Cove Scenic Area, 7M, F, 10 July 1978 (NCSM A2353).

Remarks.— Hoffman (1958) referred to the metatergal stripes as being "light pearl gray," but to my eye they are essentially white. The tricolored — black, red, and white — metaterga are diagnostic for *nantahalae* and permit accurate field determinations. Only one other southeastern xystodesmid displays white metatergal stripes, *Sigmoria leucostriata,* in Cocke County, Tennessee, but it has partially or completely white, rather than red, paranota.

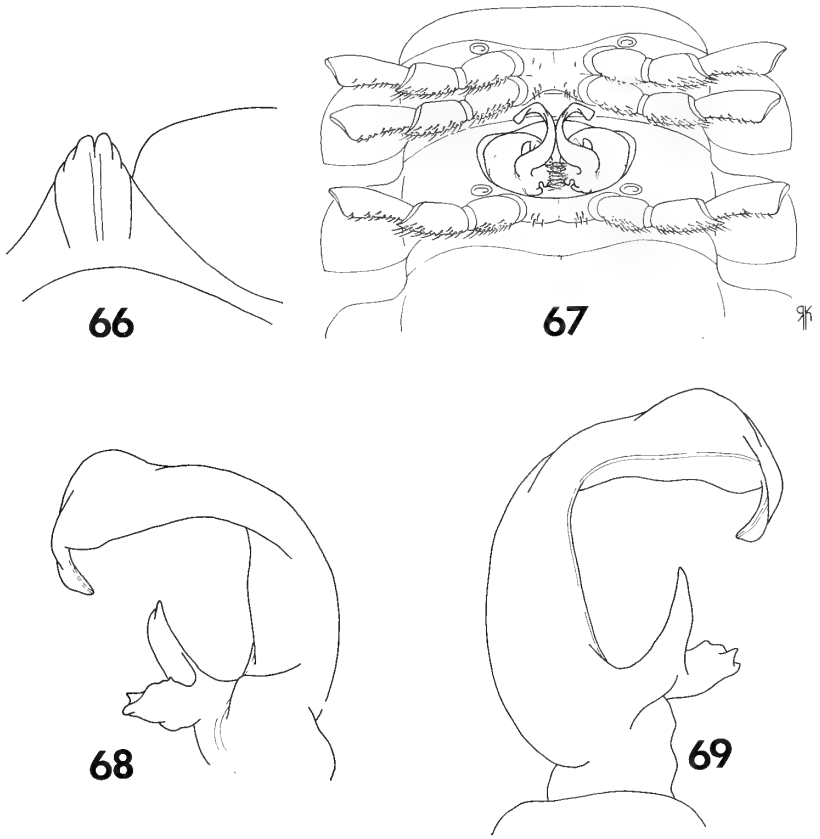
The *Translineata* Group

The *translineata* group is comprised of three dissimilar species from the GSMNP, two of which, *translineata* and *lyrea,* occur in both Tennessee and North Carolina. The only unifying anatomical feature is a divided prefemoral process, which is larger and more deeply divided in *translineata* and *lyrea.* These two species also have a rounded lobe on the lateral edge of the acropodite near the beginning of the apical curve, which may be homologous to the equivalent lobe in the *leucostriata* group and the lateral flange of species formerly in *Sigiria.* The other species, *fumimontis,* shares a medially tilted acropodite with *translineata,* which therefore exposes the lateral margin in medial view. The medial flange is long and narrow, arising on the anterior bend, extending the length of the peak, and terminating near the beginning of the apical curve; because of the tilted acropodite, the flanges of *fumimontis* and *translineata* appear wider than they actually are. The configuration of the acropodite, especially that of the distal zone, is markedly different, and the three species may not be as closely related as implied by inclusion in the same species group.

Sigmoria translineata, new species Figs. 66-69, 132-133, 136

Type specimens.— Male holotype (NCSM A1298) and 2 male and 3 female paratypes collected by R.M. Shelley and W.B. Jones, 17 May 1978, from Blount Co., Tennessee, 5.6 mi. SW Townsend, along Rich Mountain Gap Road (spur of county road 2544), just inside GSMNP boundary. Male paratype deposited in FSCA.

Diagnosis.— A large species of *Sigmoria* with medial flange on proximal portion of peak and usually with red paranota and blue transverse stripes along caudal margins of metaterga; gonopods with following diagnostic characters: acropodites usually parallel *in situ;* prefemoral process large, divided basally into two long components of variable configuration;



FIGS. 66-69, *Sigmoria translineata.* 66, process of 4th sternum of holotype, caudal view. 67, gonopods *in situ,* ventral view of paratype. 68, telopodite of left gonopod of holotype, medial view. 69, the same, lateral view. Scale line for fig. 67 = 1.00 mm; line for other figs. = 1.00 mm for each.

acropodite moderately thick and heavy, arch flattened, extending well beyond level of prefemoral process; anterior bend and apical curve sharp, latter about 90°; peak long and flattened, tilted mediad with lateral edge visible in medial view; distal zone short, extending subperpendicularly from peak, curved slightly into arch; tip simple; medial flange long and narrow, extending entire length of peak, slightly wider and rounded distally; lateral edge of acropodite with large rounded lobe proximal to apical curve.

Holotype.— Length 42.8 mm, maximum width 10.5 mm, W/L ratio 24.5%, depth/width ratio 59.0%. Segmental widths as follows:

collum	8.0 mm	8th-12th	10.5
2nd	9.1	13th-14th	10.2
3rd	9.8	15th	9.9
4th-6th	10.0	16th	9.1
7th	10.3	17th	7.9
		18th	5.9

Color in life.— paranota red; metaterga black with wide, blue, transverse stripes along caudal edges connecting paranotal spots; collum with blue stripes along both anterior and caudal edges.

Somatic features similar to those of *l. latior,* with following exceptions:

Width across genal apices 5.3 mm, interantennal isthmus 1.7 mm. Antennae reaching back to caudal edge of 3rd tergite, relative lengths of antennomeres 2>3>4>5>6>1>7. Facial setae as follows: epicranial, interantennal, and genal absent, frontal 1-1, clypeal about 15-15, labral about 29-29.

Dorsum strongly coriaceous on paranota. Collum very broad, extending well beyond ends of following tergite. Paranota mildly depressed. Caudolateral corners rounded through segment 5, becoming blunt and progressively more acute thereafter.

Process of 4th sternum (Fig. 66) moderately large, slightly shorter than width of adjacent coxae; knobs and flattened areas of 5th sternum distinct but relatively small; sternum of segment 6 convexly recessed between 7th legs to accommodate apical curvatures of acropodites, 7th legs set slightly farther apart than 6th. Postgonopodal sterna relatively flat, without lobes, with varying shallow grooves and impressions on segments 8-11 and wide, shallow central impressions on remaining segments. Coxae with low blunt tubercles beginning on segment 8, becoming sharply acute and spiniform on segments 10-16.

Gonopodal aperture broadly oval, 3.7 mm wide and 1.6 mm long at midpoint, indented on anteriolateral edge, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 67, of paratype) with acropodites touching at about midlength in midline of aperture, not overlapping, extending forward over anterior edge of aperture with apices curved laterad. Gonopod structure as follows (Figs. 68-69): prefemoral process large, divided basally into two long components, one directed mediad with broadly irregular edge, other directed sublaterad with acuminate tip, lateral component slightly longer than medial. Acropodite moderately thick and heavy, with basal spur on inner surface at distal end of prefemur, arch flattened, extending well beyond level of prefemoral process; anterior bend sharp, well defined, located proximal to 1/3 length; peak of arch relatively long and flat, tilted mediad so that outer surface visible in medial view; apical curve sharp, approximately 90°, located at about 3/4 length; distal zone short, directed almost perpendicularly from peak, only slightly curved into arch; tip blunt and simple, directed toward prefemoral process. Medial flange relatively narrow, arising on anterior bend, extending length of peak, terminating at apical curve, edge relatively straight

and smooth, slightly wider distally. Tooth absent. Lateral edge of acropodite with distinct rounded lobe opposite wider distal portion of medial flange, just proximal to apical curve. Lateral flange arising smoothly from outer lobe, relatively long and narrow, terminating proximal to tip. Prostatic groove crossing to lateral side near base of acropodite and continuing to tip.

Male paratypes.— The male paratypes agree with the holotype in all details.

Female paratype.— Length 44.3 mm, maximum width 10.4 mm, W/L ratio 23.5%, depth/width ratio 68.3%. Agreeing with male in somatic features, with following exceptions: paranota more strongly depressed creating appearance of more highly arched body; caudolateral corners of paranota rounded through segment 8; collum not extending beyond ends of following tergite.

Cyphopods *in situ* with side of receptacle visible in aperture, valves directed caudad. Receptacle moderately large, cupped around ventral end of valves, extending about halfway down sides, surface convoluted with folds and ridges. Valves moderate, surface finely granulate.

Variation.— The male from Swain County, North Carolina, collected on the north side of Fontana Dam in the GSMNP in 1978 (NCSM A1915), had red transverse stripes along the caudal edge of the paranota which were concolorous with the paranotal spots. Otherwise, all specimens I collected had red paranota and blue stripes.

The gonopods of this species are quite uniform. The shapes of the components of the prefemoral processes vary, and the distal zone is slightly longer and curves inward into the arch more on a couple of males. Details of the acropodite curvature and the flanges do not differ appreciably between individuals.

Ecology.— *Sigmoria translineata* is a cove inhabiting species.

Distribution.— Southern half of Great Smoky Mountains National Park in Swain County, North Carolina, and Blount County, Tennessee (Figs. 132, 136). The range traverses the North Carolina-Tennessee state line, and hence the specific name *translineata.* Specimens were examined as follows:

NORTH CAROLINA: *Swain Co.,* ca. 6 mi. N Cherokee, along US hwy. 441 just below Collins Cr., 2250′, GSMNP, 2M, 1 June 1962, T. Savage (RLH); and 18.8 mi. NW Bryson City, along Appalachian Trail N Fontana Dam, GSMNP, M, 23 June 1970, F.A. Coyle (WAS) and along road 0.5 mi. N jct. rd. to overlook of Fontana Lake, M, 16 May 1978 (NCSM A1915).

TENNESSEE: *Blount Co.,* 2 mi. W Townsend, along roadside, 2M, 5 May 1951, L. Hubricht (RLH); 5.6 mi. SW Townsend, along Rich Mtn. Gap Rd. (spur of co. rd. 2544), just inside GSMNP boundary, 3M, 3F, 17 May 1978 (NCSM A1928) TYPE LOCALITY; along rd. to Cades Cove ca. 1.0 mi. S jct. TN hwy. 73, at W Prong Little R. by 1st bridge after tunnel, GSMNP, M, 17 May 1978 (NCSM A1930); and Cades Cove, along Vista Tr. near campground, GSMNP, M, 2F, 18 June 1976 (NCSM A894).

Remarks.— *Sigmoria translineata* occurs sympatrically with *fumimontis,* particularly in the Cades Cove area of the GSMNP; however, they do not appear to be microsympatric since they were taken from different sections of the Cove. The two species differ in several respects, most notably the configurations of the prefemoral processes and distal zones, and gonopods

should be carefully examined before rendering determinations. The former can usually be recognized by the parallel, non-overlapping arrangement of the acropodites *in situ,* which is a key feature of *translineata.*

Sigmoria lyrea, new species Figs. 70-73, 132-133, 136

Type specimens.— Male holotype (NCSM A1920) and 4 male and 4 female paratypes collected by R.M. Shelley and W.B. Jones, 17 May 1978, from Blount Co., TN, 8.5 mi. SE Tallassee, GSMNP, along Parsons Bridge Rd., 0.1 mi. N junction with US hwy. 129, about 4 mi. W North Carolina State line. Male and female paratypes deposited in FSCA and RLH.

Diagnosis.— A large species of *Sigmoria* with medial flange on proximal portion of peak and with red paranota and blue transverse stripes along caudal margins of metaterga; gonopods with following diagnostic characters: prefemoral process large, divided basally into two long, apically acuminate, subequal components, lateral component extending beyond level of tip of acropodite; acropodite moderately thick, arch a broad continuous curve slightly overhanging prefemoral process; anterior bend and apical curve broad, poorly defined, continuous through peak; peak broadly curved, rising to apex at midlength; distal zone elongated, extending to level of prefemoral process, broadly curved into arch; tip pseudoreflexed; medial flange long and narrow, extending entire length of peak, wider proximally and distally; lateral edge with rounded lobe near beginning of apical curve; tooth and lateral flange absent.

Holotype.— Length 47.8 mm, maximum width 10.7 mm, W/L ratio 22.4%, depth/width ratio 63.6%. Segmental widths as follows:

collum	7.8 mm	8th-13th	10.7
2nd	9.0	14th	10.5
3rd	9.8	15th	10.2
4th	10.1	16th	9.4
5th-7th	10.5	17th	8.3
		18th	6.0

Color in life.— paranota red; metaterga black with wide, blue, transverse stripes along caudal edges connecting paranotal spots; collum with blue stripes along both anterior and caudal edges.

Somatic features similar to *l. latior,* with following exceptions:

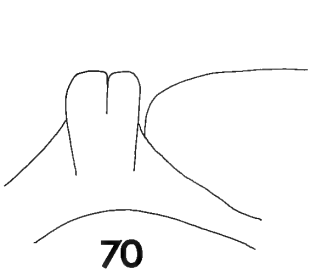
Width across genal apices 5.7 mm, interantennal isthmus 1.8 mm. Antennae moderately long and slender, reaching back to caudal edge of 3rd tergite, relative lengths of antennomeres 2>3>4>5>6>1>7. Facial setae as follows: epicranial, interantennal, and genal absent, frontal 1-1, clypeal about 14-14, labral about 18-18.

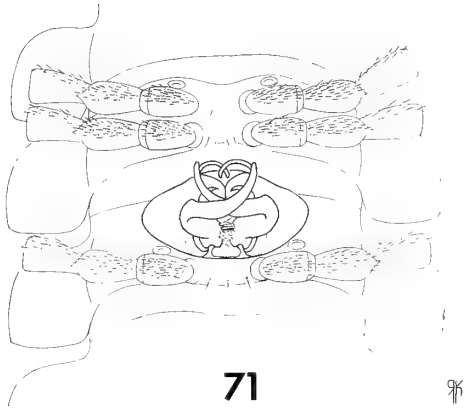
Dorsum strongly coriaceous on paranota. Paranota mildly depressed, continuing slope of dorsum. Collum broad, extending well beyond ends of following tergite. Caudolateral corners of paranota rounded through segment 6, becoming blunt and progressively more acute thereafter.

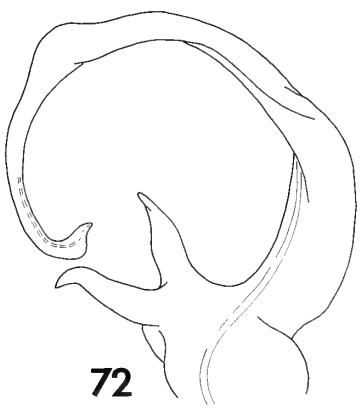
Process of 4th sternum (Fig. 70) long, subequal in length to width of adjacent coxae; knobs between 4th legs (5th sternum) coalesced medially into single, moderately long process, shorter

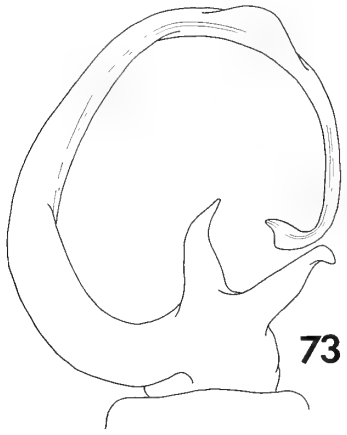
in length than width of adjacent coxae, elevated areas between 5th legs enlarged, distinct; sternum of segment 6 deeply, convexly recessed between 7th legs to accommodate gonopodal telopodites, 7th legs set slightly farther apart than 6th. Postgonopodal sterna generally flat, without lobes, with wide, shallow, central impressions. Coxae with low blunt tubercles beginning on segment 8, sharply acute and spiniform on segments 10-16.

Gonopodal aperture broadly ovoid, 4.2 mm wide and 2.2 mm long at midpoint, indented on anteriolateral edge, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 71, of paratype) with acropodites overlapping near midlength in midline of aperture, curving broadly anteriodorsad to just beyond anterior margin of aperture, tips overlapping slightly again in midline. Gonopod structure as follows (Figs. 72-73): prefemoral process large, divided basally into two long, subequal, apically acuminate components; lateral component extending beyond









FIGS. 70-73, *Sigmoria lyrea*. 70, process of 4th sternum of holotype, caudal view. 71, gonopods *in situ*, ventral view of paratype. 72, telopodite of left gonopod of holotype, medial view. 73, the same, lateral view. Scale line for fig. 71 = 1.00 mm; line for other figs. = 1.00 mm for each.

level of tip of acropodite, curved broadly mediad apically; medial component bent sharply dorsad apically. Acropodite moderately thick, arch a broad, continuous curve extending slightly beyond level of prefemoral process; basal zone bowed slightly; anterior bend broad, poorly defined, beginning around 1/4 length, continuing smoothly through peak into apical curve; peak of arch rounded, apex at midlength, extending about 1/3 of acropodite length; apical curve broad, poorly defined, beginning about 2/3 length, forming arc with wide diameter; distal zone very long, extending from peak to level of division of prefemoral process, curving broadly into arch; tip curved upwards from distal zone at level of prefemoral process division, directed toward peak of arch, pseudoreflexed. Medial flange relatively long and narrow, indistinct, not clearly demarcated from stem of acropodite, widest basally, narrowing at midlength and widening slightly distad, arising at anterior bend, terminating near apical curve. Tooth absent. Lateral edge with distinct rounded lobe near beginning of apical curve opposite wide distal portion of medial flange. Lateral flange absent. Prostatic groove running along inner surface of acropodite basally, crossing to lateral side at anterior bend and continuing to tip.

Male paratypes.— The male paratypes agree closely with the holotype in all details.

Female paratype.— Length 46.0 mm, maximum width 10.4 mm, W/L ratio 22.5%, depth/width ratio 69.2%. Agreeing essentially with male in somatic features, with following exceptions; paranota more strongly depressed creating appearance of more highly arched body; caudolateral corners of paranota rounded through segment 10; collum not extending beyond ends of following tergite.

Cyphopods *in situ* with side of receptacle visible in aperture, valves directed sublaterad. Receptacle large, cupped over ventral end of valves, extending only slightly down sides, surface convoluted with ridges and depressions. Valves relatively large, surface finely granulate.

Variation.— There is little variation among the available specimens of *lyrea*. All displayed the color pattern of the holotype, and the gonopods are virtually identical. Even the shape and relative lengths of the components of the prefemoral processes are essentially the same on all specimens. The males in Dr. Hoffman's collection differ in that the lateral component of the prefemoral process is slightly longer than the medial, the lateral lobe of the acropodite is slightly more pointed, and the apical curve is not as broad.

Ecology.— *Sigmoria lyrea* is a cove dwelling species.

Distribution.— Southern periphery of the GSMNP, along the north side of the Little Tennessee River (Figs. 132-133, 136). Specimens have been examined as follows:

NORTH CAROLINA: *Swain Co.*, 20.5 mi. WNW Bryson City (4 mi. NW Fontana Village in Graham Co.), along Twenty Mile Cr., GSMNP, 2M, F, 17 May 1978 (NCSM A1919).

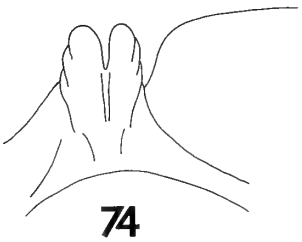
TENNESSEE: *Blount Co.*, 8.5 mi. SE Tallassee, along Parsons Br. Rd., 0.1 mi. N. jct.US hwy. 129, 4 mi. W NC state line, GSMNP, 5M, 5F, 17 May 1978 (NCSM A1920) TYPE LOCALITY; ravine 1 mi. E Calderwood, along US hwy. 129, GSMNP, 2M, 15 May 1961, L. Hubricht (RLH); and 4.8 mi. SE Tallassee, along US hwy. 129 at Tabcat Cr., 3.2 mi. SE jct. Foothills Pkwy., GSMNP, M, F, 17 May 1978 (NCSM A1922).

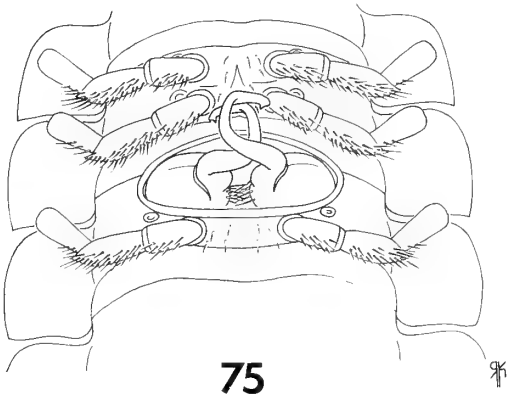
Remarks.— Although the tip of the acropodite of *lyrea* is at a sharply different angle from the distal zone and has the configuration of that of *latior,* it is continuous with the distal zone and not a separate lamina. Hence it is not truly reflexed, which would require a separate lamina as in *latior.* However, it projects at essentially the same angle as a reflexed tip and is

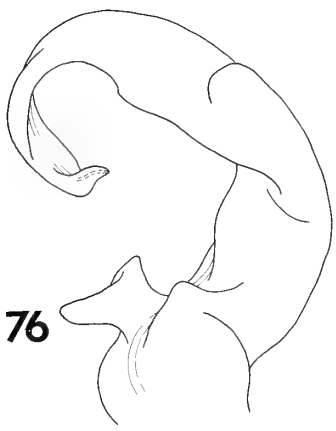
more strongly demarcated from the distal zone than the non-reflexed tips of *simplex* and *quadrata*. Thus, the tip of *lyrea* is classified as "pseudo-reflexed."

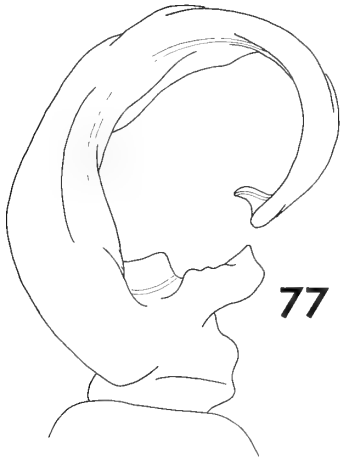
Sigmoria fumimontis, new species Figs. 74-77, 132-133, 136

Type specimens.— Male holotype (NCSM A1923) and 5 male and 4 female paratypes collected by R.M. Shelley and W.B. Jones, 17 May 1978, from Blount Co., TN, 10.5 mi. S Maryville, Abram's Creek Campground area, GSMNP, 6.8 mi. E Foothills Parkway. Male and female paratypes deposited in FSCA.









FIGS. 74-77, *Sigmoria fumimontis*. 74, process of 4th sternum of holotype, caudal view. 75, gonopods *in situ*, ventral view of paratype. 76, telopodite of left gonopod of holotype, medial view. 77, the same, lateral view. Scale line for fig. 75 = 1.00 mm; line for other figs. = 1.00 mm for each.

Diagnosis.— A large species of *Sigmoria* with medial flange on proximal portion of peak and with stripes along caudal margins of metaterga; gonopods with following diagnostic characters: prefemoral process short, apically expanded mediad and laterad, subbifurcate; acropodite thick and massive, stem very wide; peak of arch tilted mediad, exposing lateral edge in medial view; distal zone extending well into arch under distal extremity of medial flange; medial flange long and narrow; tooth absent.

Holotype.— Length 46.8 mm, maximum width 11.5 mm, W/L ratio 24.6%, depth/width ratio 63.5%. Segmental widths as follows; segments 14-15 damaged and unmeasurable:

collum	8.3 mm	13th	11.1
2nd	9.4	16th	10.0
3rd	10.1	17th	8.6
4th-6th	11.0	18th	6.1
7th-12th	11.5		

Color in life: paranota red; metaterga black with light blue transverse stripes along caudal edges connecting paranotal spots; collum with blue stripes along both anterior and caudal borders.

Somatic features similar to *I. latior,* with following exceptions:

Width across genal apices 5.8 mm, interantennal isthmus 1.9 mm. Antennae extending back to caudal edge of third segment, relative lengths of antennomeres 2>3>4>5=6>1>7. Facial setae as follows: epicranial, interantennal, frontal, and genal absent, clypeal about 15-15, labral about 18-18.

Collum moderately broad, extending slightly beyond ends of following tergite on each side.

Process of 4th sternum (Fig. 74) large, nearly equal in length to width of adjacent coxae; paramedial knobs of 5th sternum between 4th legs relatively large, flattened areas between 5th legs produced into knobs subequal to those between 4th legs; sternum of segment 6 slightly recessed between 6th legs, deeply and convexly recessed between 7th legs to accommodate curvature of telopodites. Postgonopodal sterna without lobes, with varying narrow grooves and impressions on segments 8-11 and one large, shallow, central impression on remaining segments.

Gonopodal aperture ovoid, 4.3 mm wide and 2.1 mm long at midpoint, indented on anteriolateral edge, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 75, of paratype) with acropodites overlapping at midlength in midline and again at apical curve region, extending forward over anterior edge of aperture and between 7th legs. Gonopod structure as follows (Figs. 76-77): coxa relatively large. Prefemur relatively small, with blunt lobe apically in midline; prefemoral process short but apically wide with central depression (subbifurcate), expanded into short lateral and relatively long medial projections, directed away from acropodite. Acropodite thick and massive, stem wide in cross section, arch extending well beyond level of prefemoral process; anterior bend well defined, about 90°, located near 1/3 length; peak flattened but angled upwards to apex at apical curve, relatively long, greater than 1/3 acropodite length, tilted mediad exposing lateral edge in medial view; apical curve well defined, beginning at about 2/3 length, forming arc with broad diameter; distal zone long, extending well into arch and underlying distal extremity of medial flange, directed toward base of acropodite; tip reflexed. Medial flange long and narrow, only slightly wider than, and poorly demarcated from, stem of acropodite, arising near base of anterior bend, terminating abruptly just distal to midlength of peak. Tooth absent. Lateral flange relatively long and wide, beginning about midlength of distal zone, expanding gradually with termination proximal to tip of

acropodite. Prostatic groove running along inner surface of acropodite, crossing to lateral side proximal to base of anterior bend and continuing to tip.

Male paratypes.— The male paratypes agree with the holotype in all particulars.

Female paratype.— Length 48.5 mm, maximum width 11.1 mm, W/L ratio 22.9%, depth/width ratio 73.0%. Agreeing essentially with holotype in somatic features; paranota only slightly more depressed than in male, much less depressed than in females of other species of *Sigmoria.*

Cyphopods *in situ* with side of receptacle visible in aperture, valves directed dorsocaudad. Receptacle large, hook like, cupped over ventral end of valves, extending completely around lateral side and halfway down medial side of valves, surface convoluted with folds and ridges. Valves with surface finely granulate.

Variation.— The gonopods of *fumimontis* are quite uniform, and the only noticeable variation involves the prefemoral process. On most males this structure is not really bifurcate, being greatly expanded apically into long lateral and medial lobes. There is, however, a slight central depression on the outer edge of the process suggesting bifurcation, hence the term subbifurcate. On the males from Cades Cove the structure is definitely bifurcate, with the two components directed generally toward the end of the acropodite. The apical curve on these individuals is also slightly narrower.

Ecology.— *Sigmoria fumimontis* is a cove dwelling species.

Distribution.— Known only from Blount County, Tennessee, where it occurs from Maryville east to Cades Cove in the Great Smoky Mountains National Park (Figs. 132, 136). The species has been collected along several small creeks and rivers in this area, but it seems to be most common along Abrams Creek in the Park. Specimens have been examined as follows:

TENNESSEE: *Blount Co.,* Maryville, 3M, F, November 1929, O.F. Cook (RLH); 12 mi. SW Maryville, along Ninemile Cr. at 1st bridge on 2425, 0.5 mi. S jct. US hwy. 129, 2M, F, 11 October 1978 (NCSM A2465); 6.4 mi. SE Maryville, near small tributary of Dunlap Br. on unmarked rd., 2 mi. N. jct. Foothills Pkwy, M, 3F (NCSM A2461); 10.5 mi. S Maryville, Abrams Cr. campground GSMNP, 6.8 mi. E Foothills Pkwy., 6M, 5F, 17 May 1978 (NCSM A1923) TYPE LOCALITY; 4 mi. W Townsend, along Little R. on TN hwy. 73 in GSMNP, M, F, 17 May 1978 (NCSM A1924); and along trail to log cabin near Abrams Falls, Cades Cove Area, GSMNP, 2M, 3F, 18 June 1976 (NCSM A893).

Remarks.— Although the gonopods are similar in overall configuration to species of the *latior* group, the affinities of *fumimontis* are believed to be with *translineata* and *lyrea* because of their geographic proximities and the tilted acropodite, also demonstrated by *translineata.* The occurrence of a more deeply divided prefemoral process in the population of *fumimontis* in Cades Cove, where it is geographically closest to *translineata,* is further evidence of relationship with this group rather than with *latior.*

The *Bidens* Group

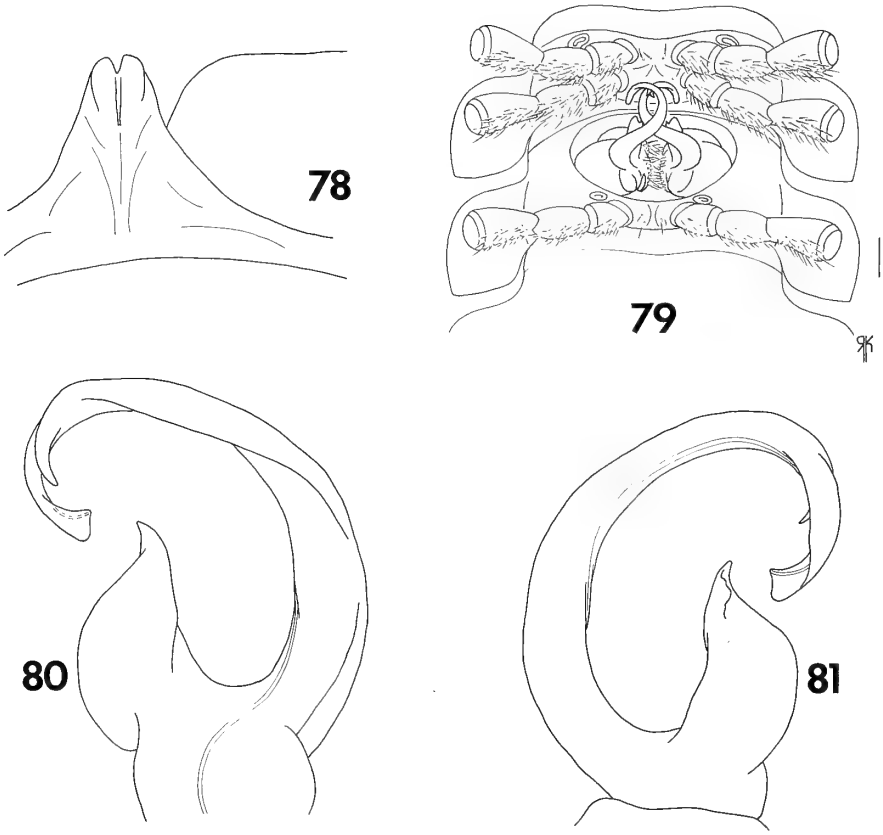
The *bidens* group contains only the one species, whose affinities are obscure. The uniquely shaped prefemoral process tends to separate it from

the *translineata* group, which is geographically closest, and the location of the tooth on the distal zone rather than on the peak, excludes it from the *latior* group. *Sigmoria bidens* occurs only in Sevier County, Tennessee, near the main entrance to the GSMNP.

Sigmoria bidens (Causey), new combination Figs. 78-81, 132-133, 136

Apheloria bidens Causey, 1942:169-170, fig. 9.
Dixioria bidens: Causey, 1950:6. Wray, 1967:152.
Falloria bidens: Chamberlin and Hoffman, 1958:33.

Type specimens.— Male holotype and female allotype (ANSP Type #11263) collected by N.B. Causey, 21 June 1940, from Sevier Co., TN,



FIGS. 78-81, *Sigmoria bidens*. 78, process of 4th sternum of holotype, caudal view. 79, gonopods *in situ*, ventral view of topotype. 80, telopodite of left gonopod of holotype, medial view. 81, the same, lateral view. Scale line for fig. 79 = 1.00 mm; line for other figs. = 1.00 mm for each.

Chimneys Picnic Area, Great Smoky Mountains National Park, along US hwy. 441, circa 7.3 mi. S Gatlinburg. According to Causey (1942) 3 female paratypes were taken at the same time and place, but their current location is unknown.

Diagnosis.— A moderate-size species of *Sigmoria* with medial flange on proximal portion of peak and with red paranota and usually blue transverse stripes along caudal margins of metaterga; gonopods with following diagnostic characters: prefemoral process greatly enlarged, subglobose basally, extending to or beyond level of tip of acropodite; acropodite relatively wide basally, becoming much thinner at anterior bend; anterior bend broad, poorly defined, beginning near base of acropodite; medial flange long and narrow, extending most of length of peak, poorly demarcated from stem of acropodite; tooth subconical usually widely separated from flange, located on distal zone; tip slightly reflexed, directed toward midlength of basal zone.

Holotype.— Length 41.0 mm, maximum width 9.4 mm, W/L ratio 22.9%, depth/width ratio 60.6%. Segmental widths as follows:

collum	7.2 mm	11th-14th	9.2
2nd	8.2	15th	8.7
3rd	8.6	16th	8.0
4th	8.9	17th	6.9
5th-10th	9.4	18th	5.3

Color in life (from Causey 1942): paranota bright red; metaterga dark brown; head and antennae lighter brown; distal half of legs red; venter and proximal half of legs pale yellow. This notation was obviously taken from faded, preserved material, and Causey did not mention metatergal stripes in her description.

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 5.0 mm, interantennal isthmus 1.9 mm. Antennae long and slender, reaching back to caudal edge of 3rd metatergum, relative lengths of antennomeres 2=6>3=5>4>1>7. Facial setae as follows: epicranial, interantennal, frontal, and genal not detected; clypeal about 10-10, labral about 8-8.

Collum not extending beyond ends of following tergite. Paranota depressed, continuing slope of dorsum, caudolateral corners rounded on segments 1-5, squared on 6-13, and becoming progressively more pointed posteriorly. Peritremata distinct on segments 4-18 but only slightly elevated above paranotal surface.

Process of 4th sternum moderate in size (Fig. 78), subequal in length to width of adjacent coxae; knobs and elevated areas of 5th sternum moderate in size; sternum of segment 6 convexly recessed between 7th legs to accommodate curvature of telopodites. Postgonopodal sterna generally flat and unmodified, bicruciately impressed on segments 8-9 and with shallow, rounded, central impressions on 10-16. Coxae with low blunt tubercles on legs of segments 11-17.

Gonopodal aperture relatively large and ovoid, 3.9 mm wide and 2.0 mm long at midpoint, indented slightly along anteriolateral edge, margins slightly elevated above metazonal surface. Gonopods *in situ* (Fig. 79, of topotype) with acropodites overlapping at about midlength in midline of aperture and again at region of apical curve, extending forward over anterior edge of aperture to between 7th legs. Gonopod structure as follows (Figs. 80-81): prefemoral pro-

cess greatly enlarged, extending to level of tip of acropodite, subglobose basally, bifurcate apically, components acuminate and subequal in length but lateral one wider. Acropodite relatively wide basally, becoming thin and narrow distal to anterior bend, arch extending beyond and overhanging prefemoral process; anterior bend relatively broad and poorly defined, beginning near base of acropodite; peak of arch relatively long and flattened but gradually rising to apex at beginning of apical curve; apical curve relatively broad and poorly defined, forming arc with relatively broad diameter; distal zone moderate in length, broadly curving inward into arch; tip slightly reflexed, projecting inward from distal zone, directed toward midlength of basal zone. Medial flange relatively long and narrow, poorly demarcated from stem of acropodite, arising near base of anterior bend and terminating at start of apical curve, obscuring only small section of stem of acropodite. Tooth present, acuminate and subconical, displaced distad and clearly separated from medial flange, located at about 1/3 length of distal zone. Lateral flange long and narrow, beginning at apical curve and terminating just proximal to tip. Prostatic groove running along inner face of acropodite basally, crossing to lateral side at anterior bend and continuing to tip.

Male topotypes.— The topotypes that I collected at Chimneys Picnic Area (NCSM A1888) had red paranota with wide, blue, transverse connecting stripes along the caudal margins of the metaterga and both the anterior and caudal margins of the collum. The blue stripes in this sample were distinct and quite different from the black metatergal base color.

The males in this sample are somewhat variable in size, some being much smaller in length and width than the holotype.

The gonopods of these males differ slightly from those of the holotype in the configuration of the prefemoral process and medial flange. The former structures tend to be less globose basally and more distinctly bifurcate apically, although the bifurcation is not always visible in medial view. The medial flange is much narrower than that of the holotype and is only slightly wider than the acropodite stem.

Female allotype.— Length 42.7 mm, maximum width 10.3 mm, W/L ratio 24.1%, depth/width ratio 69.9%. Agreeing essentially with males in somatic features except paranota more strongly depressed creating impression of more highly arched body.

Cyphopods *in situ* with receptacle visible in aperture, valves directed caudolaterad. Receptacle cupped around ventral end of valves, extending slightly down both sides, surface with deep grooves and folds. Valves moderately large, surface mildly grooved.

Variation.— The color of *bidens* varies; specimens from along US highway 441, 1.3 mi. E Chimneys Picnic Area (NCSM A1903) had red paranota and red stripes, whereas those from the Elkmont Campground area (NCSM A1936) had pink peritremata, but the rest of the paranota and the stripes were dark purple. All other specimens were the same colors as the topotypes.

The most significant gonopodal variation involves the prefemoral process. The structure is always much larger basally, but it is irregularly shaped rather than subglobose on some specimens. The apical bifurcation also changes, and the medial component is longer on some males. Individuals from near Elkmont campground possess the longest prefemoral processes, as the longer medial components extend beyond the level of the tip of the acropodites. Other gonopodal variation includes the length of the peak of the arch and the general curvature of the acropodite. The peak is typically flat, so that the structure overhangs and extends well beyond the level of the

prefemoral process. The male from Gatlinburg (FSCA), however, is more highly arched with a relatively short peak, and consequently the acropodite barely extends beyond the prefemoral process.

Ecology.— *Sigmoria bidens* is a cove dwelling species. It is common in moist litter at the Chimneys Picnic area, and most of the specimens I collected were under thin layers of leaves on pavement or relatively hard soil. The edges of litter, where the cover is sometimes slightly deeper and moister, seem to be preferred, and most of the specimens seem to occur in the outer 8 inches to 1 foot of litter.

Distribution.— Headwater valleys of the Little River and West Fork of the Little Pigeon River in eastern Sevier County, Tennessee (Figs. 132-133). Most of the known localities are in the GSMNP, where the species ranges from near Gatlinburg to the Elkmont Campground (Fig. 136). The male from Porter Creek Flats in the Park, cited by Causey (1950), is in the FSCA collection, but the label in the vial merely states, "Gatlinburg, cove hardwoods." Porter Creek is not on any map available to me, and although it must be near Gatlinburg, the precise location is unknown. *Sigmoria bidens* is absent from North Carolina, despite its listing by Wray (1967). Specimens were examined as follows:

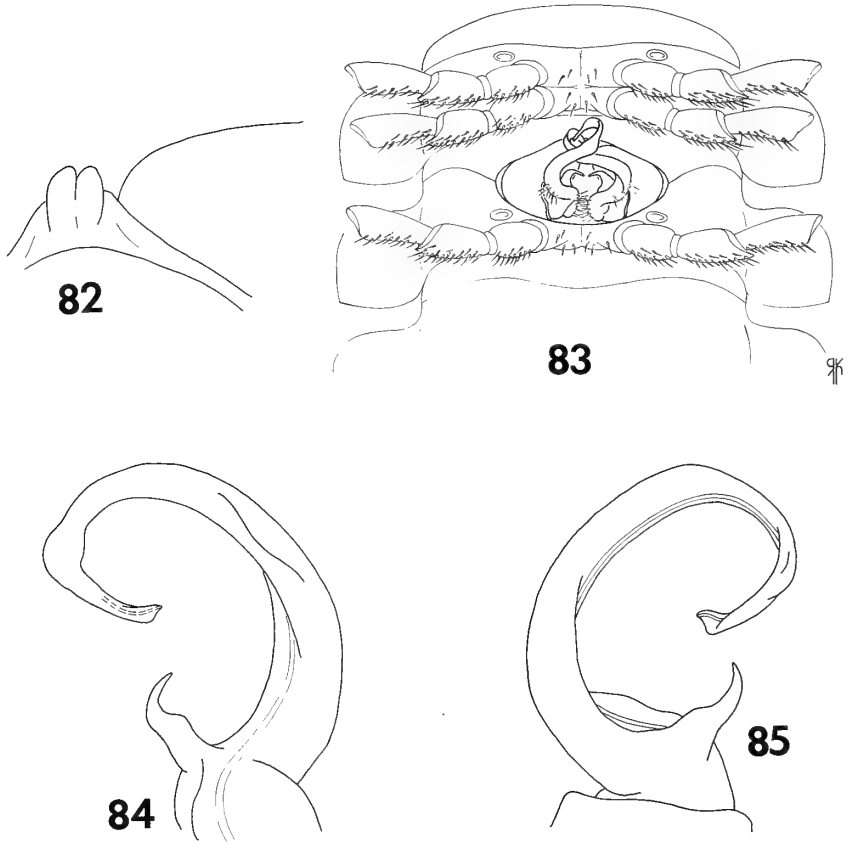
TENNESSEE: *Sevier Co.,* along US hwy 441, 6 mi. S Gatlinburg, 3 mi. N Chimneys Picnic Area, GSMNP, 2M, 2F, 16 May 1978 (NCSM A1898); GSMNP, along US hwy. 441, 6.25 mi. SE Gatlinburg, 1.3 mi. E Chimneys Picnic Area, 5M, 2F, 16 May 1978 (NCSM A1903); 7.3 mi. S Gatlinburg, Chimneys Picnic Area, off US hwy. 441, 3.7 mi. E jct. TN hwy. 73, GSMNP, M, F, 21 June 1940, N.B. Causey (ANSP Type #11263), along nature trail near picnic grounds, M, 2 May 1959, F.W. Mead (FSCA), 2M, 30 May 1962, T. Savage (RLH), and 6M, 8F, 16 May 1978 (NCSM A1888) TYPE LOCALITY; Sugarlands Nature Trail, jct. US hwy. 441 and TN hwy. 73, near GSMNP Park Headquarters, 2M, 2F, 16 May 1978 (NCSM A1894); along Little R. Trail, 0.1 mi. E Elkmont Cpgd., GSMNP, 5M, 2F, 19 May 1978 (NCSM A1936); GSMNP entrance on US hwy. 441 at Gatlinburg, M, 7 May 1980 (NCSM A3001); 2.5 mi. ENE Gatlinburg, jct. Roaring Fork Nature Trail and Cherokee Orchard Rd., GSMNP, M, 7 May 1980 (NCSM A3002); 2 mi. ENE Gatlinburg, Junglebrook area on Cherokee Orchard Rd., GSMNP, 2M, 2F, 8 May 1980 (NCSM A3003); and Gatlinburg, cove hardwoods, M, 24 June, 1947, H. Hansen (FSCA).

Remarks.— With an overlapping *in situ* gonopodal configuration, a flattened peak of the arch, a medial flange and tooth, and an apical lateral flange, *bidens* demonstrates ample features of *Sigmoria* to be accommodated by this genus. The general acropodal pattern is that of the *latior* group, but the species differs in several particulars, notably the thin nature of the acropodite distal to the anterior bend; the broad, poorly defined anterior bend; the thicker, subconical tooth and its location on the distal zone rather than on the peak; the slightly reflexed tip with only a slight angle from the distal zone; and the enlarged prefemoral process. The magnitude of these differences and their geographic separation suggest that

bidens is probably not closely related to *latior,* and *bidens* is therefore placed in a group by itself. The tooth appears to have evolved independently in *latior* and *bidens,* whereas the enlarged subglobose prefemoral process is a specialization peculiar to the latter.

The *Leucostriata* Group

The two species of the *leucostriata* group are characterized by a greatly reduced medial flange, a broadly curved or sharply bent (at midlength) distal zone which extends into the arch, a small medial and larger lateral lobe opposite each other on the proximal half of the distal zone, and a pseudoreflexed tip. The medial and lateral lobes are believed to represent



FIGS. 82-85, *Sigmoria leucostriata.* 82, process of 4th sternum of holotype, caudal view. 83, gonopods *in situ,* ventral view of paratype. 84, telopodite of left gonopod of holotype, medial view. 85, the same, lateral view. Scale line for fig. 83 = 1.00 mm; line for other figs. = 1.00 mm for each.

reduced medial and lateral flanges of species formerly in *Sigiria,* and, with a small medial flange on the proximal portion of the peak, this group thus displays features of both *Sigiria* and *Sigmoria,* necessitating their synonymy. The millipeds are moderate to large in size, and *leucostriata* usually exhibits white paranota and white metatergal stripes, while *xerophylla* displays the red paranota and blue stripe pattern. The group ranges south along the western fringe of the Blue Ridge Province from the French Broad River in Cocke County, Tennessee, to the southern extremity of the mountains in Gilmer County, Georgia.

Sigmoria leucostriata, new species Figs. 82-85, 132-133

Type specimens.— Male holotype (NCSM A1953) and 3 male and 6 female paratypes collected by R.M. Shelley and W.B. Jones, 19 May 1978, from Cocke Co., Tennessee, 10 mi. S Newport, CNF, along county road 2485, 4 mi. N junction with I-40. Male and female paratypes deposited in FSCA.

Diagnosis.— A moderate-size species of *Sigmoria* with small medial flange on proximal portion of peak and round medial and lateral lobes on distal zone; usually with white paranota and white transverse stripes along caudal margins of metaterga; gonopods with following diagnostic characters: prefemoral process moderate in length, not extending to level of tip of acropodite, narrowing at midlength, apically acuminate; anterior bend and apical curve broad, poorly defined, continuous through gently curved peak; distal zone long, bent sharply inward into arch at midlength, with rounded medial and lateral lobes at bend; tip pseudoreflexed; medial flange very short and narrow, poorly demarcated from stem of acropodite, not obscuring section of acropodite; lateral flange present, long and narrow.

Holotype.— Length 40.1 mm, maximum width 10.3 mm, W/L ratio 25.7%, depth/width ratio 58.3%. Segmental widths as follows:

collum	7.1 mm	10th-13th	10.3
2nd	8.1	14th	10.0
3rd	9.0	15th	9.8
4th	9.7	16th	9.0
5th-9th	10.0	17th	7.8
		18th	5.8

Color in life: paranota white with pink peritremata; metaterga black with wide, white, transverse stripes along caudal edges connecting paranotal spots; collum with white stripes along both anterior and caudal edges.

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 4.9 mm, interantennal isthmus 1.4 mm. Antennae reaching back to middle of 3rd tergite; relative lengths of antennomeres $2>3>4=5=6>1>7$. Facial setae

as follows: epicranial, interantennal, and genal absent; frontal 1-1, clypeal about 12-12, labral about 18-18.

Dorsum smooth, polished, becoming mildly coriaceous on paranota. Collum moderate, extending only slightly beyond ends of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 6, becoming blunt and progressively more acute thereafter.

Process of 4th sternum (Fig. 82) shorter than width of adjacent coxae; knobs and flattened areas of 5th sternum distinct but relatively small; 6th sternum convexly recessed between 7th legs to accommodate apical curvatures of acropodites, 7th legs set slightly farther apart than 6th. Postgonopodal sterna relatively flat, without lobes, with varying shallow grooves and impressions, including wide central impression on segments 10-17. Coxal tubercles beginning on segment 8, becoming sharply acute and spiniform on segments 11-17.

Gonopodal aperture ovoid, 3.5 mm wide and 1.8 mm long at midpoint, indented on anteriolateral edge, sides flush with metazonal surface. Gonopods *in situ* (Fig. 83, of paratype) with acropodites overlapping at about midlength in midline of aperture and extending forward beyond anterior margin of aperture, apices curving towards each other and crossing in midline. Gonopod structure as follows (Figs. 84-85): prefemoral process moderately long, narrowing and curved ventrad at midlength, apically acuminate. Acropodite moderately thick, broadly and continuously curved, overhanging and extending well beyond level of prefemoral process; anterior bend broad, poorly defined, beginning around 1/4 length; peak gently curved, continuous with anterior bend and apical curve, apex around midlength; apical curve beginning around 2/3 length, broad, poorly defined; distal zone relatively long, bent abruptly inward into arch at midlength, with slight lobe on medial side at level of bend opposite larger, more rounded lateral lobe, latter visible in medial view; tip pseudoreflexed, directed toward anterior bend. Medial flange short and narrow, inconspicuous, poorly demarcated from and not obscuring stem of acropodite. Tooth absent. Lateral flange long and narrow, arising at beginning of apical curve, terminating proximal to tip. Prostatic groove running along inner surface of acropodite basally, crossing to lateral side at anterior bend and continuing to tip.

Male paratypes.— The male paratypes agree closely with the holotype in all particulars.

Female paratype.— Length 41.9 mm, maximum width 11.1 mm, W/L ratio 26.6%, depth/width ratio 65.8%. Agreeing essentially with holotype in somatic features except paranota more strongly depressed, creating appearance of more highly arched body.

Cyphopods *in situ* with side of receptacle visible in aperture, valves directed caudolaterad. Receptacle large, rugulose, cupped around ventral end of valves, extending nearly completely down sides of valves, surface convoluted with deep folds and ridges. Valves large, surface finely granulate.

Variation.— The paranotal color of *leucostriata* varies. In samples NCSM A1957 and A2447 they are entirely white and do not have pink peritremata as in the type specimens. The white paranotal color is concolorous with that of the stripes. Material from Sevier County had light yellow paranota and stripes.

The gonopods vary in several respects. The prefemoral process is different in each sample, being shortest in the male in NCSM A2447, in which the structure is not bent ventrad at the narrowing point. On the acropodite of this male the arch is longer, the peak flatter, and the inward bend of the distal zone sharper, so that the structure overhangs the prefemoral process more than in the other samples. The medial lobe in this male is reduced from that in the holotype, but the lateral lobe is larger and more broadly

rounded. The medial flange is subsimilar in all males, and the pseudoreflexed tip is present on all specimens.

Ecology.— Sigmoria leucostriata is a cove dwelling species.

Distribution.— Known only from the CNF in eastern Cocke and Sevier counties, Tennessee (Fig. 132). The species appears to be restricted to the south side of the French Broad River (Fig. 133). Specimens were examined as follows:

TENNESSEE.— *Cocke Co.,* 2 mi. NE Newport, French Broad River bluffs, CNF, M, F, 18 May 1961, L. Hubricht (RLH); 9.5 mi. E Newport, Bear Bridge Rd., 2.5 mi. W jct. TN hwy. 107, CNF, 5F, 19 May 1978 (NCSM A1957); 10 mi. S Newport, along co. rd. 2485, 4 mi. N jct. I-40, CNF, 4M, 6F, 19 May 1978 (NCSM A1953) TYPE LOCALITY; and 7.5 mi. S Newport, rd. off TN hwy. 32 just inside boundary of CNF, M, 9 October 1978 (NCSM A2447); *Sevier Co.,* 13.5 mi. SE Sevierville, along unmarked rd. beside Dunn R., 3M, 8 May 1980 (NCSM A3014).

Remarks.— The white or light yellow paranota and concolorous metatergal stripes are diagnostic for *leucostriata* and permit reliable field identifications. The only other apheloriine species with white stripes is *nantahalae,* which has red paranota and occurs in North Carolina well removed from the range of *leucostriata.*

The configuration of the medial lobe at the bend of the distal zone is similar to that of the medial flange in *nigrimontis intermedia* from Madison County, North Carolina, adjacent to Cocke County, Tennessee. The two structures appear to be homologous, and hence the conclusion that *Sigiria* is a synonym of *Sigmoria.*

Sigmoria xerophylla, new species Figs. 86-89, 132-133, 138

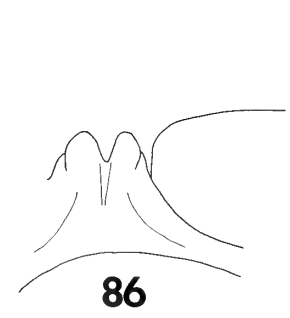
Type specimens.— Male holotype (NCSM A2491) and 8 male and 2 female paratypes collected by R.M. Shelley and W.B. Jones, 14 October 1978, from McMinn Co., TN, 8 mi. S Athens, along county road 4374, 1.1 mi. E junction of county road 4372. Male paratype deposited in FSCA.

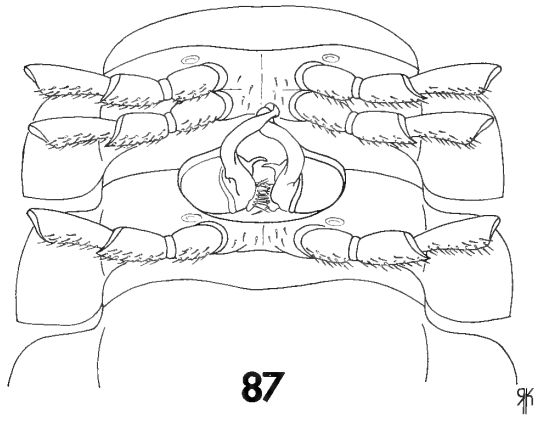
Diagnosis.— A large species of *Sigmoria* with small medial flange on proximal portion of peak and medial and lateral lobes on distal zone, with red paranota and blue transverse stripes along caudal margins of metaterga; gonopods with following diagnostic characters: prefemoral process moderately long, bent ventrad at midlength, apically acute; anterior bend broad, poorly defined; apical curve sharper; peak long and gently curved, apex near midlength; distal zone curved broadly into center of arch, not bent abruptly at midlength, with moderate proximal medial lobe opposite large lateral lobe; tip pseudoreflexed; medial flange very short and narrow, poorly demarcated from and not obscuring stem of acropodite; lateral flange absent.

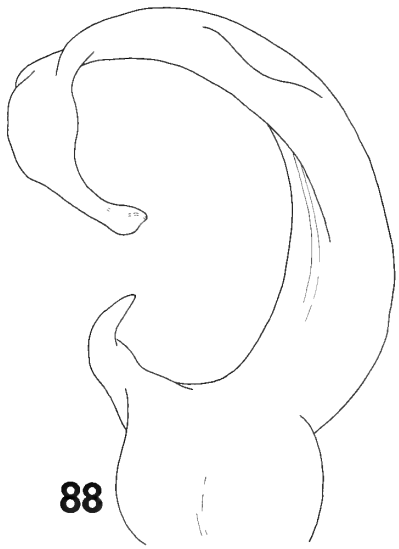
Holotype.— Length 42.6 mm, maximum width 11.3 mm, W/L ratio 26.5%, depth/width ratio 57.6%. Segmental widths as follows:

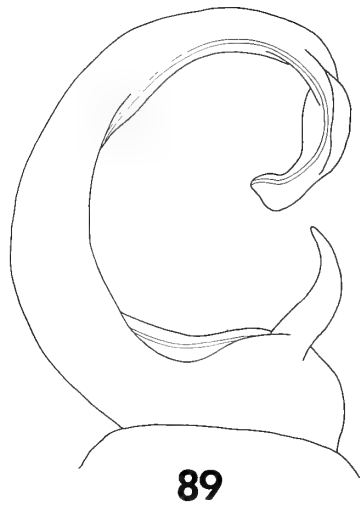
collum	7.8 mm	7th-14th	11.3
2nd	9.6	15th	10.9
3rd	10.0	16th	10.1
4th	10.5	17th	8.7
5th-6th	11.0	17th	6.0

Color in life: paranota red; metaterga black with wide, blue transverse stripes along caudal









FIGS. 86-89, *Sigmoria xerophylla*. 86, process of 4th sternum of holotype, caudal view. 87, gonopods *in situ*, ventral view of specimen from 2.7 mi. SE Reliance, Polk Co., Tennessee. 88, telopodite of left gonopod of holotype, medial view. 89, the same, lateral view. Scale line for fig. 87 = 1.00 mm; line for other figs. = 0.75 mm for 86, 1.00 mm for 88-89.

edges connecting paranotal spots; collum with blue stripes along both anterior and caudal edges.

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 5.3 mm, interantennal isthmus 1.7 mm. Antennae reaching back to caudal edge of 3rd tergite, relative lengths of antennomeres 2>3>4=5=6>1>7. Facial setae as follows: epicranial, interantennal, and frontal absent, genal 1-1, clypeal about 14-14, labral about 18-18.

Dorsum smooth, polished, becoming mildly coriaceous on paranota. Collum moderate, extending slightly beyond ends of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 5, becoming blunt and progressively more acute posteriorly.

Process of 4th sternum (Fig. 86) short, double, much shorter than widths of adjacent coxae; knobs and flattened areas of 5th sternum distinctly elevated, latter long and narrow; 6th sternum convexly recessed between 7th legs to accommodate apical curvatures of acropodites. Postgonopodal sterna relatively flat, with varying shallow grooves and impressions, particularly narrow groove between leg pairs and wide central impression. Coxal tubercles beginning on segment 9 and ending on segment 17, low and rounded on all legs.

Gonopodal aperture ovoid, 4.1 mm wide and 1.8 mm long at midpoint, indented anteriolaterally, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 87, not this specimen) with acropodites overlapping at midlength of peak in midline of aperture, extending forward beyond anterior margin of aperture, apices curving towards each other and crossing in midline. Gonopod structure as follows (Figs. 88-89): prefemoral process moderately long, bent ventrad at midlength, directed toward anterior bend. Acropodite moderately thick, broadly curved, overhanging and extending well beyond level of prefemoral process; anterior bend broad, poorly defined, beginning near 1/4 length; peak gently curved, continuous with anterior bend, about 1/3 of acropodite length, apex near midlength; apical curve beginning about 2/3 length, moderately well defined, sharper than anterior bend; distal zone relatively long, curved broadly inward into arch, with moderate lobe on proximal portion of medial edge opposite larger lateral lobe, latter visible in medial view; tip pseudoreflexed, directed toward anterior bend. Medial flange short and narrow, inconspicuous, poorly demarcated from and not obscuring stem of acropodite. Tooth and lateral flange absent. Prostatic groove running along inner surface of acropodite basally, crossing to lateral side at anterior bend and continuing to tip.

Male paratypes.— The male paratypes agree essentially with the holotype in all particulars.

Female paratype.— Length 41.0 mm, maximum width 10.3 mm, W/L ratio 25.1%, depth/width ratio 68.9%. Agreeing closely with holotype in somatic features, except paranota more strongly depressed, creating appearance of more highly arched body.

Cyphopods *in situ* with side of receptacle visible in aperture, valves directed caudolaterad. Receptacle large, rugulose, cupped around ventral end of valves, extending nearly completely down sides of valves, surface convoluted with deep folds and ridges. Valves large, surface finely granulate.

Variation.— The gonopods of *xerophylla* are quite uniform, with the only significant variation involving the acropodite arch. Two males from McMinn County (NCSM A2490) have a much flatter arch, and the acropodites extend farther beyond the level of the prefemoral process. The prefemoral process, medial flange, and lobes on the distal zone are subsimilar on all individuals.

Ecology.— *Sigmoria xerophylla* is a cove inhabitant, usually occurring

under thin layers of leaves on hard substrates near water sources. However, on two occasions in Polk County it was found in very dry leaf piles under rhododendron bushes. The leaves were covered with a fine, white dust, and the substrates under the piles were sandy. The specific name refers to its occurrence in this habitat.

Distribution.— Southwestern edge of the Blue Ridge Province in southeastern Tennessee and north Georgia, ranging from McMinn and Monroe counties, Tennessee, to Gilmer County, Georgia (Fig. 132). The species appears to be restricted to south of the Little Tennessee River (Fig. 133). Specimens were examined as follows:

TENNESSEE: *McMinn Co.,* 8.8 mi. N Athens, along co. rd. 4272 at Sewee Cr., 2M, 3F, 14 October 1978 (NCSM A2490); and 8 mi. SW Athens, along co. rd. 4374, 1.1 mi. E jct. co. rd. 4372, 9M, 2F, 14 October 1978 (NCSM A2491) TYPE LOCALITY. *Monroe Co.,* 13.5 mi. NE Benton in Polk Co., along co. rd. 2518 at Polk Co. line, CNF, M, F, 13 October 1978 (NCSM A2480). *Polk Co.,* 4 mi. N Benton, along unnumbered rd. at Chestee R., M, 13 October 1978 (NCSM A2486); 2.7 mi. SE Reliance, Lost Creek Cpgd., CNF, 3M, 2F, 7 July 1978 (NCSM A2337); 3.2 mi. SE Reliance, along unnumbered rd., 0.5 mi. E Lost Creek Cpgd., CNF, F, 7 July 1978 (NCSM A2336); 0.6 mi. W Archville, along co. rd. 4314 at Greasy Cr., CNF, 3M, 3F, 8 July 1978 (NCSM A2338); 2 mi. E Ocoee, ravine, M, 13 May 1961, L. Hubricht (RLH); Sugar Loaf Mtn., near Parksville, CNF, M, F, 10 May 1964, L. Hubricht (RLH); and 2.5 mi. SE Parksville, along unnumbered rd. at Chilowhee Cpgd., 0.3 mi. NW US hwy. 64, CNF, M, 2F, 8 July 1978 (NCSM A2341).

GEORGIA: *Gilmer Co.,* 10 mi. NW Ellijay, along US Forest Service rd. 68 near Barnes Creek Picnic Area, Chattahoochee Nat. For., 3M, 3F, 8 July 1978 (NCSM A2344); and 5 mi. NW Ellijay, along US hwy. 76 at Mountaintown Cr., Chattahoochee Nat. For., 3M, F, 4 June 1975, R.L. Hoffman (RLH).

Remarks.— This species is very similar to *leucostriata* and could be interpreted as a subspecies of the latter. I consider it a species, however, due to the different color, the absence of a lateral flange, and the absence of intergrade specimens. Since *xerophylla* does not occur north of the Little Tennessee River, this boundary may have served to isolate it from *leucostriata* to the north.

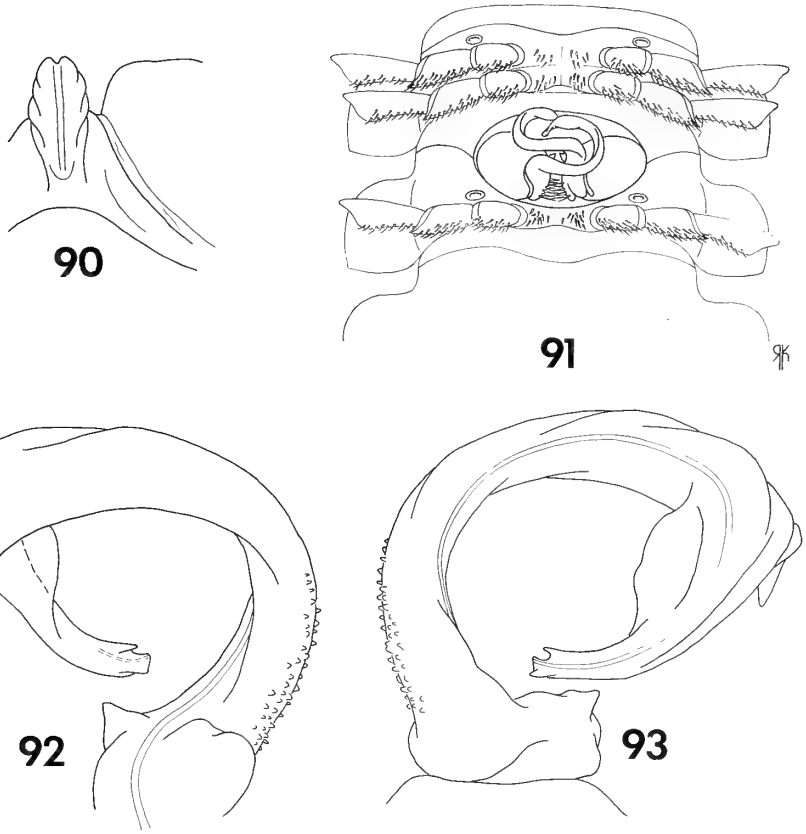
The *Tuberosa* Group

As with *bidens*. the affinities of *tuberosa* are obscure, and it is placed in a group by itself. The species possesses a number of unique features including hirsute postgonopodal sterna, a circular gonopodal aperture, tubercles on the basal zone, fusion of the tooth and medial flange, an additional flange on the inner surface of the distal zone, and a complex tip. The only congeners which are geographically proximal to *tuberosa* are *rubromarginata rubromarginata,* which is sympatric at Smokemont, and *translineata,* which also occurs in the Oconaluftee Valley.

Sigmoria tuberosa, new species Figs. 90-93, 132-133, 136

Type specimens.— Male holotype (NCSM A1879) and 10 male and 4 female paratypes collected by R.M. Shelley and W.B. Jones, 15 May 1978, from Swain Co., NC, Smokemont Campground, along US highway 441 ca. 7 mi. N Cherokee, GSMNP. Two male paratypes (RLH) collected by L. Hubricht, 22 June 1960, from same locality. Male and female paratypes deposited in FSCA.

Diagnosis.— A large species of *Sigmoria* with medial flange on proximal portion of peak and with red paranota and blue transverse stripes along caudal margins of metaterga; gonopods with following diagnostic characters: basal zone with numerous minute tubercles on outer surface;



FIGS. 90-93, *Sigmoria tuberosa.* 90, process of 4th sternum of holotype, caudal view. 91, gonopods *in situ,* ventral view of paratype. 92, telopodite of left gonopod of holotype, medial view. 93, the same, lateral view. Scale line for fig. 91 = 1.00 mm; line for other figs. = 1.00 mm for each.

tooth fused to distal extremity of medial flange; distal zone elongated, extending into arch nearly to base of acropodite at level of prefemoral process, with wide, thin lamella on inner surface projecting into arch and continuing for about 2/3 length; tip complex, apex blunt, with subterminal lobe on medial edge, lateral edge reflexed outward away from arch.

Holotype.— Length 44.1 mm, maximum width 10.0 mm, W/L ratio 22.7%, depth/width ratio 64.0%. Segmental widths as follows:

collum	7.5 mm	13th-14th	9.8
2nd	8.3	15th	9.4
3rd	9.1	16th	8.7
4th	9.5	17th	7.5
5th-9th	9.9	18th	5.5
10th-12th	10.0		

Color in life: paranota red; metaterga black with wide, blue transverse stripes along caudal edges connecting paranotal spots; collum with blue stripes along both anterior and caudal edges.

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 5.2 mm, interantennal isthmus 1.8 mm. Antennae long and slender, reaching back to middle of 4th tergite, relative lengths of antennomeres $2>3>5=6>4>1>7$. Facial setae as follows: epicranial and interantennal absent, frontal 1-1, genal 2-2, clypeal about 12-12, labral about 24-24.

Dorsum with very little wrinkling in paranotal regions. Collum broad, extending well beyond ends of following tergite. Caudolateral corners of paranota rounded on segments 1-10, becoming blunt and progressively more acute thereafter.

Process of 4th sternum (Fig. 90) large, longer than width of adjacent coxae; processes of 5th sternum large, paramedial knobs between 4th legs subequal in length to width of adjacent coxae, elevated areas between 5th legs slightly smaller than knobs and shorter than width of adjacent coxae; sternum of segment 6 only slightly depressed between 7th legs. Postgonopodal sterna with relatively dense tufts of hairs on caudal edges, clusters in patches beside posterior leg coxae, becoming thinner and smaller posteriorly, smaller, thinner patches beside anterior coxae; sternal surfaces relatively flat, without lobes, with varying shallow grooves and impressions. Coxae without tubercles.

Gonopodal aperture relatively rounded, 4.1 mm wide and 2.8 mm long at midpoint, not indented anteriolaterally, sides low, flush with metazonal surface. Gonopods *in situ* (Fig. 91, of paratype), with acropodites overlapping at about 1/3 length and curving around one another in subparallel fashion, extending only slightly over anterior margin of aperture. Gonopod structure as follows (Figs. 92-93): coxa relatively large. Prefemur relatively small, with sharp lobe apically in midline; prefemoral process small, subtriangular. Acropodite relatively thick, arch a tight, nearly circular curve, subflattened at peak, overhanging and extending well beyond level of prefemoral process; basal zone with numerous minute tubercles on outer surface, continuing to level of anterior bend, diminishing in number distally; anterior bend sharp, well defined, located at about 1/4 length; peak of arch relatively long and subflattened, about 1/2 length of acropodite, tilted slightly mediad; apical curve sharp and well defined, forming arc with relatively wide diameter; distal zone long, curved broadly into arch, extending nearly to base of acropodite just above level of prefemoral process, with wide, thin lamella on inner surface arising proximally and continuing for about 2/3 length of zone, lamella projecting well into arch; tip blunt, complex in structure, with subterminal lobe on medial edge, lateral edge slightly reflexed outward, away from arch. Medial flange thick and heavy, arising at anterior

bend, widening continuously to fusion with tooth. Tooth fused to distal extremity of medial flange, relatively long, apically acute. Lateral flange absent, represented by thick, rounded, heavily sclerotized rim on outer edge of acropodite, arising at apical curve and continuing for half length of distal zone. Prostatic groove running along inner surface of acropodite, crossing to lateral side at anterior bend and continuing to inner corner of blunt part of tip.

Male paratypes.— The male paratypes agree essentially with the holotype in most details, excepting that the prefemoral process is a small nub in a couple of specimens.

Female paratype.— Length 44.9 mm, maximum width 10.7 mm, W/L ratio 23.8%, depth/width ratio 72.0%. Agreeing essentially with holotype in somatic features, with following exceptions: paranota more strongly depressed, creating appearance of more highly arched body; coxae with short, sharp spines on segments 6-16.

Cyphopods *in situ* with side of receptacle visible in aperture, valves directed subdorsad. Receptacle large, hood-like, cupped over ventral end of valves, with wide lobe extending down lateral side of valves and thin one extending down medial, surface with low, rounded ridges. Valves moderate, surface finely granulate.

Variation.— The gonopods of this species are rather consistent, and the only noticeable variation involves the size of the tubercles and the size and shape of the prefemoral process. The tubercles are small on all males, but on some they are larger than those on the holotype. Likewise, the prefemoral process is a small, subtriangular wedge-shaped structure on all individuals, except the male from Mingus Mill (NCSM A1878), in which it is larger and has several small, apical teeth.

Ecology.— *Sigmoria tuberosa* is a cove dwelling species.

Distribution.— Swain County, North Carolina, where it is endemic to a small area in the Oconaluftee River valley in the eastern Great Smoky Mountains National Park and the adjacent part of the Cherokee Indian Reservation (Figs. 132, 136). The milliped does not occur at high elevations and disappears well before US highway 441 starts climbing to Newfound Gap. Specimens were examined as follows:

NORTH CAROLINA: *Swain Co.*, 4.4 mi. NW Smokemont, along unnumbered rd., 3.3 mi. NW jct. US hwy. 441, GSMNP, 5F, 16 May 1978 (NCSM A1884); 2.3 mi. NW Smokemont, along Collins Cr. at picnic area, GSMNP, M, 16 May 1978 (NCSM A1883); Smokemont Cpgd., GSMNP, along US hwy. 441, ca. 7 mi. N Cherokee, 11M, 4F, 15 May 1978 (NCSM A1879) and 2M, 22 June 1950, L. Hubricht (RLH) TYPE LOCALITY; 2 mi. E Smokemont, along Tow String Rd., 1 mi. N jct. US hwy. 441, GSMNP, M, F, 15 May 1978 (NCSM A1875); 2.5 mi. S Smokemont, vicinity of Mingus Mill, 0.1 mi. W jct. US hwy. 441, GSMNP, M, 15 May 1978 (NCSM A1878); and along US hwy. 441 W Cherokee, M, August 1952, R.W. Lichtwardt (RLH).

Remarks.— *Sigmoria tuberosa* possesses more unique features than any congener. To begin with, the body is very stiff, rigid, and fragments easily; the other species of *Sigmoria* are more flexible and pliable, and are much easier to handle both in the field and laboratory.

Ventrally, the process of the 4th sternum of *tuberosa* is the largest in the genus, being longer than the widths of the 3rd coxae. The hirsute nature of the postgonopodal sterna is also unique, since only a few scattered setae oc-

cur on the caudal edge of the sterna in most species of *Sigmoria*. The sternal surface therefore appears to be glabrous. In *tuberosa,* however, dense clusters of setae occur on the caudal edges near the posterior coxae, and smaller, thinner patches occur near the anterior coxae. These patches become smaller and thinner posteriorly, and disappear around segment 16.

On the gonopods the configuration of the acropodite of *tuberosa* is different from that of any congener. No other species has tubercles on the basal zone, an inward projecting lamella on the distal zone, and a complex tip. The distal zone of *tuberosa* is the most complex in *Sigmoria,* with a tripartite tip and an entirely new process, the lamella on the inner surface. Unlike other species the reflexed portion of the tip in *tuberosa* is on the lateral rather than the medial edge, and it projects away from the arch instead of into it. Moreover, the reflexion does not carry the groove, which opens on the inner corner of the blunt part of the tip. Also in *tuberosa* the gonopod tooth is fused to the distal extremity of the medial flange. In *areolata,* the only other species with the tooth on the lamella of the medial flange, it is well separated from the lobe of the flange and appears to be a separate structure.

A final unique feature of *tuberosa* concerns the gonopodal aperture. It is more rounded than that of other species and is the only one without an indentation on the anteriolateral edge and with the sides flush with the metazonal surface.

Obviously no congener is closely related to *tuberosa,* and the species represents a distinct phylogenetic line. For a long time I considered placing it in a monotypic genus, and I have also tried, unsuccessfully, to relate it elsewhere, for example with *Cleptoria divergens* and species of *Dynoria.* However, direct comparisons of the gonopods of *tuberosa* with those of these millipeds revealed no homologies and few general similarities. In truth, *tuberosa* has more in common with species of *Sigmoria* than with any other southeastern xystodemids. The gonopod curves in a basic *Sigmoria* pattern and has a short prefemoral process, medial flange, and tooth. Moreover, the *in situ* configuration, with the telopodites overlapping and lying transversely over the opposite side of the aperture, is a characteristic *Sigmoria* pattern. Therefore, I consider *tuberosa* a species of *Sigmoria* that represents a distinct phylogenetic line, and since nothing resembling it has ever been collected, there has probably been considerable extinction in this line. There is still a slim chance that a relative may survive in remote, isolated areas of the GSMNP, just as *tuberosa* does in the Oconaluftee Valley. Until such a form is discovered, however, *tuberosa* must be considered the sole survivor of an entire branch of apherloriine evolution.

The *Rubromarginata* Group

The two species of the *rubromarginata* group are characterized by large flanges, both on the distal zone in *rubromarginata,* and the lateral on the peak in *triangulata.* They lack a medial flange on the proximal portion of the peak. The distal zone tapers to an acuminate tip and is either bent sharply (90°) inward into the arch near midlength (termination point of the flanges) or is bisinuately curved. Thus, the tip is directed toward the basal zone in *rubromarginata* and dorsad (downward in medial view) toward the prefemoral process in *triangulata.* The acropodite is highly arched with a gently curved peak, so that the overall configuration of the telopodite resembles a question mark (?). The species of this group occur from eastern Tennessee (Greene to Sevier counties) to the South Mountains of Burke, Cleveland, and Rutherford counties, North Carolina, but are concentrated in the middle French Broad River Valley.

Sigmoria rubromarginata (Bollman), new combination Fig. 134

Diagnosis.— A moderate-size species of *Sigmoria* with medial flange on distal zone opposite lateral flange, and with red paranota and red metatergal stripes; gonopods with following diagnostic characters: arch high and rounded, shaped like question mark, acropodite extending to level of prefemoral process; flanges large and conspicuous, lateral one with margin broadly rounded; distal zone tapering to acuminate tip, bent inward into arch at about right angle near midlength or termination point of flanges.

Ecology.— *Sigmoria rubromarginata* is a cove dwelling species.

Remarks.— This colorful milliped was the first species described that is referable to *Sigmoria.* The name alludes to the red stripe along the caudal edge of each metatergite and the anterior edge of the collum but this condition occurs in many congeners and in other "sigmoid" xystodesmid genera, and is not diagnostic of *rubromarginata.* The species ranges from the western edge of the Blue Ridge Province in Cocke and Sevier counties, Tennessee, to the South Mountains in the western Piedmont Plateau of Burke and Cleveland counties, North Carolina. Two geographic races have evolved, one chiefly in the French Broad River basin of North Carolina and eastern Tennessee, and the other in the South Mountain Range, which is one of five major inselberg mountain regions in piedmont North Carolina (Filka and Shelley 1980a). Intergrade populations occur along the edge of the Blue Ridge escarpment and in the adjacent lowlands of the western Piedmont. The two subspecies of *rubromarginata* can be distinguished as follows:

Gonopods in medial view showing profile of arch and distal zone; edge of medial flange visible in medial view, face directed dorsad; prefemoral process relatively long, recurved at midlength and directed toward basal zone, simple or bifurcate, one component usually much longer when bifurcate (Fig. 97); middle French Broad River basin of western North Carolina and eastern Tennessee, and adjacent fringe of Little Tennessee basin in North Carolina ..... *rubromarginata rubromarginata* (Bollman)

Distal zone twisted about 90° mediad, revealing faces of medial and lateral flanges in medial view; proximal portion of arch visible, distal obscured by flanges; bend of distal zone directed away from field of vision in medial view and obscurred by flanges; prefemoral process relatively short and straight, usually bifurcate, components subequal (Fig. 102); South Mountain Range of Burke, Cleveland, and Rutherford counties, North Carolina ..... *rubromarginata austrimontis,* new subspecies.

Sigmoria rubromarginata rubromarginata (Bollman), new status

Figs. 94-99, 134-136

Fontaria rubromarginata Bollman, 1887:622. Attems, 1938:167. Brimley, 1938:498.

Sigiria rubromarginata: Hoffman, 1950b:25. Chamberlin and Hoffman, 1958:48. Wray, 1967:152.

Sigiria scorpio Chamberlin 1939:9, figs. 26-27. Chamberlin, 1940b:56. Wray, 1967: 152.

Sigmoria zyga Chamberlin, 1949:3, fig. 2. Hoffman, 1950a:7. Chamberlin and Hoffman, 1958:51. Wray, 1967:152. **NEW SYNONYMY.**

Type specimen.— Male holotype (NMNH 320) collected by George T. Atkinson on unspecified date from Balsam, Jackson Co., North Carolina.

Diagnosis.— Distinguished by following features of gonopod; prefemoral process relatively long, recurved at midlength and directed toward basal zone, simple or bifurcate with one component usually much longer than other; acropodite with profile of arch, distal zone, and edge of medial flange visible in medial view, face of medial flange directed dorsad.

Holotype.— Other species of the *rubromarginata* and *nigrimontis* groups will be compared to this description:

Length 35.1 mm, maximum width 9.4 mm, W/L ratio 27.1%, depth/width ratio 55.7%. Segmental widths as follows:

collum	6.4 mm	6th-14th	9.5
2nd	7.8	15th	8.9
3rd-4th	8.6	16th	8.4
5th	9.1	17th	7.2
		18th	5.6

Color in life: anterior border of collum and posterior margins of other segments red (Bollman 1887).

Head capsule smooth, polished; width across genal apices 4.6 mm; interantennal isthmus 1.4 mm. Epicranial suture distinct, extending to interantennal region. Antennae long and slender, extending to middle of paranota of fourth segment, becoming progressively more hirsute distally; first antennomere subglobose, 2-6 clavate, 7 short and truncate; relative lengths of antennomeres $2>3>5=6>4>1>7$. Genae not margined laterally, trace of central impression, ends broadly rounded and extending slightly beyond adjacent margins of cranium. Facial setae

as follows: epicranial, interantennal, frontal, and genal not detected; clypeal about 6-6, irregularly spaced; labral about 10-10, varying in length.

Dorsum smooth, polished, becoming mildly coriaceous in paranotal regions. Collum large, broad, extending slightly behind ends of following tergite on each side. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded on segments 1-7, becoming slightly blunt on 8-9 and progressively more acute posteriorly. Peritremata relatively flat on all segments, only slightly elevated above paranotal surface; scapulorae distinct and cup shaped; ozopores situated just caudal to midlength of peritremata, opening dorsad. Prozonites smaller than metazonites; strictures moderately distinct, slightly costulate.

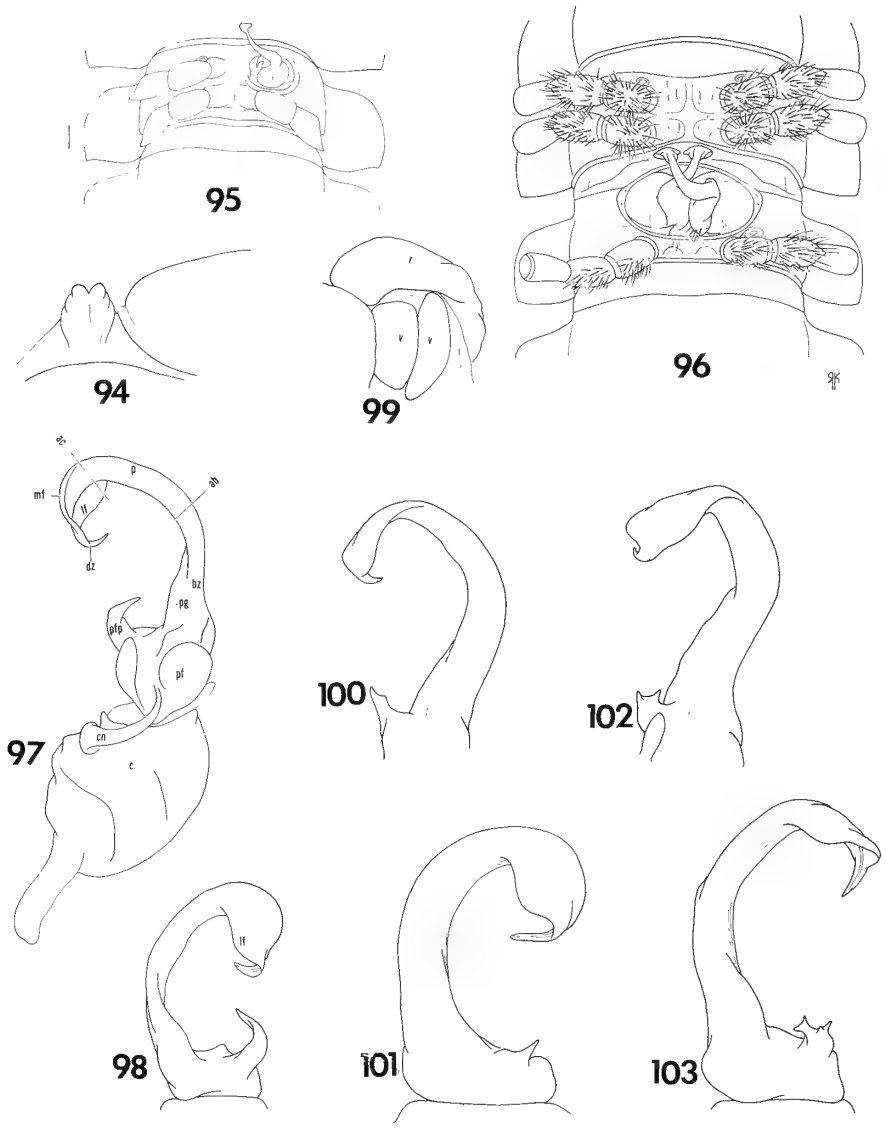
Caudal segments normal for family.

Sides of metazonites irregular, with varying shallow, curved impressions. Strictures broad, distinct. Sternum of segment 4 (Fig. 94) produced into two small, digitiform lobes, fused in midline, much shorter than width of adjacent 3rd coxae; that of segment 5 with two small lobes between 4th legs and two broad elevated flattened areas between 5th legs; sternum of segment 6 abnormal, flat and unmodified (see topotype description for normal condition). Postgonopodal sterna glabrous, with transverse grooves between leg pairs and broad, medial, longitudinal groove proximal to caudal edge. Coxae with slight distomedial tubercle beginning on segment 9, becoming distinct on 11-12, fading out on segments 17-18; prefemoral spines distinct on legs 9-30, indistinct on first eight legs; tarsal claws sigmoidally curved; pregonopodal legs much more hirsute than postgonopodal ones. Hypoproct broad, slightly subtriangular; paraprocts with edges strongly thickened.

Gonopodal condition abnormal, only left one present, normal walking leg on right side (Fig. 95), an example of hysterotely described and discussed by Shelley (1977b). Gonopodal aperture not in midline, restricted to left side, round, anterior margin flush with metazonal surface, posterior edge elevated and thickened. Gonopod structure as follows (Figs. 97-98): prefemoral process acuminate, recurved at midlength and directed toward basal zone. Acropodite moderately thin and fragile, highly arched and rounded, extending to level of prefemoral process; basal zone widest basally; anterior bend sharp, well defined, located at about 1/3 length; peak rounded, continually rising to apex at distal extremity; apical curve relatively broad, beginning at about 2/3 length; distal zone moderately long, bent abruptly (90°) inward into center of arch near midlength, or termination point of flanges; tip sharply acuminate. Medial flange with only medial edge visible in medial view, relatively large, arising at beginning of apical curve, terminating at inward bend of distal zone. Lateral flange larger than and located opposite medial, arising at beginning of apical curve, terminating at inward bend of distal zone, margin broadly rounded. Prostatic groove running along inner surface of basal zone, crossing to lateral side at anterior bend and continuing to tip.

Male topotype.— The male topotype has frontal and genal setae in the amounts of 1-1 and 3-3, respectively. The following comments describe the normal condition of the gonopodal aperture and the gonopods *in situ,* since the holotype is abnormal in these respects. Gonopodal aperture rounded, about 2.8 mm wide and 2.0 mm long at midpoint, indented slightly anteriolaterally, margins elevated above metazonal surface and thickened. Gonopods *in situ* (Fig. 96, not this specimen) with acropodites crossing in midline of aperture at about midlengths of peaks, extending anteriad slightly beyond anterior margin of aperture. The topotype gonopod is virtually identical to that of the holotype, indicating that the genetic problem in the latter did not affect the configuration of this appendage. On segment 6 of the topotype, the sternum is convexly recessed between the 7th legs to accommodate the apical curvatures of the acropodites when the body segments are compressed.

Female topotype.— Length 35.4 mm, maximum width 9.1 mm, W/L ratio 25.7%, depth/width ratio 70.3%. Agreeing essentially with holotype in somatic features, with follow-



FIGS. 94-103, *Sigmoria rubromarginata*. 94-99, *S. r. rubromarginata*. 94, process of 4th sternum of specimen from 5.7 mi. NW Brevard, Transylvania Co., North Carolina. 95, 7th segment of holotype, ventral view. 96, gonopods *in situ,* ventral view of specimen from Haywood Co., North Carolina. 97, left gonopod of holotype, medial view. 98, telopodite of the same, lateral view. 99, left cyphopod of topotype, submedial view. 100-101, intergrade, specimen from east side of Black Mountain (town), Buncombe Co., North Carolina. 100, telopodite of left gonopod, medial view. 101, the same, lateral view. 102-103, *S. r. austrimontis,* holotype.

ing exceptions; paranota more strongly depressed, giving appearance of more highly arched body; midbody sterna relatively flat, with shallow, rounded, central impressions.

Cyphopods (Fig. 99) with moderately large receptacle, cupped around ventral end of valves, extending halfway down medial and completely down lateral sides, surface finely granulate, with minute folds. Valves relatively small, outer one ovoid and slightly larger, inner one rounded, surface finely granulate.

Variation.— The gonopods of this subspecies vary in several details. The lateral flange, always much larger than the medial, is bilobed on a few individuals in the western part of the range (Madison County, North Carolina, and Cocke County, Tennessee). Likewise, the size of the medial flange varies, being larger and more clearly demarcated from the stem of the acropodite in a few scattered individuals from Swain, Haywood, and Madison counties, North Carolina, and Cocke County, Tennessee. The distal zone, bent inward into the arch on most specimens, is straight and bisinuately curved in a few. The gonopods of these individuals resemble those of *triangulata* but can be identified as *r. rubromarginata* by the configuration of the lateral flanges. In males in which the prefemoral process is bifurcate, the components are always unequal in length, and the longer one is always bent backwards toward the basal zone. In specimens from the western fringe of the range (Cocke and Sevier counties, Tennessee, and western Haywood County, North Carolina) the arch is flatter, and the acropodites overhang the prefemoral process in medial view.

Distribution.— *Sigmoria r. rubromarginata* occurs mostly in the middle French Broad basin of western North Carolina and eastern Tennessee, south and west of the French Broad River (Fig. 135). It also occurs in the adjacent fringe of the Little Tennessee basin in Swain and Jackson counties, North Carolina. It does not cross the French Broad River, and is replaced on the northern side by *triangulata* and *nigrimontis intermedia.* Specimens were examined as follows:

NORTH CAROLINA: *Swain Co.,* 2 mi. NE Bryson City, entrance to GSMNP at Deep Creek area, along co. rd. 1339, 1.2 mi. W jct. co. rd. 1375, 6M, 2F, 16 May 1978 (NCSM A1905); 2.8 mi. NW Bryson City, along co. rd. 1329, 0.4 mi. W jct. co. rd. 1331, 2M, 16 May 1978 (NCSM A1907); Smokemont Cpgd., GSMNP, M, 22 June 1950, L. Hubricht (RLH); bridge to Smokemont Cpgd., GSMNP, 4M, F, 15 May 1978 (NCSM A1873); and 8.5 mi. NE Cherokee, GSMNP, along park rd., 14.9 mi. W Heintooga Overlook, M, 2F, 9 July 1976 (NCSM A955). *Jackson Co.,* Balsam, M, date unknown, G.T. Atkinson (NMNH 320) and M, 2F, 3 August 1949, R.L. Hoffman (RLH) TYPE LOCALITY; Soco Falls, PNF, M, 20 May 1957, W.T. Keeton, W.C. Lund, and R.L. Hoffman (RLH); 3 mi. NW Sylva, along co. rd. 1388, 0.2 mi. N jct. US hwys. 19A and 441, M, 10 July 1976 (NCSM A967); and 7.8 mi. ESE Cullowhee, along co. rd. 1137, 2F, 10 July 1976, R.M. Shelley (NCSM A959). *Transylvania*

102, telopodite of left gonopod, medial view. 103, the same, lateral view. Scale lines for figs. 95-96 = 1.00 mm for each; line for other figs. = 1.00 mm for 94 and 102-103, 0.83 mm for 97-98 and 100-101, and 0.75 mm for 99. Abbreviations as in figs. 1-9.

Co., 9.2 mi. NNW Rosman, along US For. Serv. rd. #140, 0.6 mi. NW jct. NC hwy. 215, PNF, M, 3F, 10 September 1978, W.B. Jones (NCSM A2437); and 5.7 mi. NW Brevard, along US For. Serv. Rd. #475, 1.8 mi. W Fish Hatchery, PNF, 2M, 3F, 29 August 1973 (NCSM 1967). *Haywood Co.,* 4 mi. SE Canton, along co. rd. 1901, 0.4 mi. E jct. co. rd. 1854, PNF, 2F, 12 September 1977 (NCSM A1735); 4 mi. NW Maggie, along co. rd. 1300, M, 9 July 1976 (NCSM A945); 6.6 mi. N Canton, along co. rd. 1503, 2.3 mi. N jct. co. rd. 1508, M, 2F, 12 September 1977 (NCSM A1734); Wagon Rd. Gap, PNF, 2M, 5 June 1952, collector unknown (RLH); 11.5 mi. NNW Clyde, along co. rd. 1344, 2.0 mi. W jct. co. rd. 1338, PNF, M, F, 12 September 1977 (NCSM A1733); 16.6 mi. NNW Canton, along US For. Serv. Rd. #148, Harmon Den Wildlife Management Area, PNF, M, 8 July 1976 (NCSM A942); and 3.2 mi. SW Waterville, Big Creek Cpgd., off co. rd. 1397, GSMNP, 2M, 5F, 8 July 1976 (NCSM A930). *Madison Co.,* 9.6 mi. SSW Marshall, along NC hwy. 63, 3.5 mi. S jct. NC hwy. 209, M, 3F, 12 September 1977 (NCSM A1732); Rocky Bluff Recreation Area, PNF, M, 11 September 1977 (NCSM A1685); along NC hwy. 209 at Betsey's Gap, 3,900′, M, F, 2 August 1962, R.L. Hoffman (RLH); between Hot Springs and Paint Rock, PNF, 2M, 2F, 7 August 1910, R.V. Chamberlin (RVC) and 2M, 2F, 2 August 1962, R.L. Hoffman (RLH, WAS); and 3.3 mi. W Hot Springs, along co. rd. 1303, 4M, F, 10 May 1980, L. Peacock (NCSM A3022).

TENNESSEE: *Cocke Co.,* Cosby Picnic Area, GSMNP, 8M, 5F, 19 June 1976 (NCSM A903) and 5M, 3F, 19 May 1978 (NCSM A1944); along Indian Camp Cr. W Cosby, GSMNP, 2M, 8 May 1980 (NCSM A3011); 11.5 mi. S Newport, along rd. to Caton's Grove, CNF, 2M, 2F, 19 May 1978 (NCSM A1948); 12 mi. SE Newport, along co. rd. 2485 near Sandy Gap, CNF, 3M, 19 May 1978 (NCSM A1954); 9.5 mi. E Newport, along Bear Branch Cr., 2.5 mi. W jct. TN hwy. 107, CNF, M, 19 May 1978 (NCSM A1958); along 1st rd. off US hwys. 25-70 W NC state line, CNF, 2M, 2F, 19 May 1978 (NCSM A1960); 4.8 mi. S Newport, along co. rd. 2418, CNF, 6M, 2F, 4 juvs., 9 October 1978 (NCSM A2444); 12 mi. SW Newport, along TN hwy. 32, CNF, 2M, 3F, 10 October 1978 (NCSM A2459); and 4.8 mi. SW Newport, along Carson Springs Rd., 2.3 mi. W jct. I-40, 10 October 1978 (NCSM A2453). *Sevier Co.,* along Rhododendron Cr. in Greenbrier area of GSMNP, 1.8 mi. S jct. TN hwy. 73, M, 19 May 1978 (NCSM A1943); 7.5 mi. NE Gatlinburg, along TN hwy. 73 near Pittman, CNF, 2M, F, 8 May 1980 (NCSM A3009); and east slope of Big Ridge W Gatlinburg, CNF, M, F, 8 August 1961, collector unknown (FSCA).

Remarks.— Chamberlin (1939) thought that the configuration of the distal zone, bending inward into the arch, resembled the stinger of a scorpion, and hence his specific name, *"scorpio."*

Sigmoria rubromarginata austrimontis, new subspecies Figs. 102-103, 134

Type specimens.— Male holotype (NCSM A661) and 11 male and 4 female paratypes collected by R.M. Shelley and J.C. Clamp, 14 August 1975, from Burke Co., NC, 9.2 mi. S Valdese, along county road 1900, 1.8 mi. W junction of county road 1924. Male and female paratypes deposited in FSCA and RLH.

Diagnosis.— Distinguished by following characters of gonopod: prefemoral process short, straight, usually bifurcate, components subequal; distal zone of acropodite twisted approximately 90° mediad, revealing faces of medial and lateral flanges in medial view; inward bend of distal zone obscured by flanges in medial view.

Variation.— The gonopods of this subspecies are more uniform than those of the nominate. The lateral flange ranges from broadly rounded to squarish, but the most variable detail is the configuration of the prefemoral process. While generally short, straight, and bifurcate, it is shaped differently on nearly every specimen. The length of the components vary, being longer and more clearly demarcated from the base of the process in some individuals. In a few males the prefemoral process is simple and not bifurcate, and in one it is trifurcate.

Distribution.— This form is restricted to the South Mountain range of Burke, northern Cleveland, and northern Rutherford counties, North Carolina (Fig. 134), one of five major inselberg mountain regions in the Piedmont Plateau of the state (Filka and Shelley 1980a). Specimens were examined as follows:

NORTH CAROLINA: *Cleveland Co.,* 4.4 mi. NW Casar, along co. rd. 1535, 1.2 mi. N jct. co. rd. 1536, 8M, 5F, 14 August 1975 (NCSM A601). *Burke Co.,* 8.1 mi. S Morganton, along co. rd. 1919, 1.3 mi. S jct. co. rd. 1918, 2M, F, 27 May 1972 (NCSM 990); 4.8 mi. SW Morganton, along co. rd. 1922, 0.4 mi. S jct. co. rd. 1936, 8M, F, 26 July 1975 (NCSM A660); 9.2 mi. S Valdese, along co. rd. 1900, 1.8 mi. W jct. co. rd. 1924, 12M, 4F, 14 August 1975 (NCSM A661) TYPE LOCALITY; 10.4 mi. S Valdese, along co. rd. 1904, 2.4 mi. W jct. co. rd. 1901, M, F, 14 August 1975 (NCSM A659); and South Mountains State Park, 3M, 3F, 9 May 1980 (NCSM A3020). *Rutherford Co.,* 17.7 mi. NE Rutherfordton, along co. rd. 1732, 1.8 mi. N jct. co. rd. 1733, 4M, F, 7 May 1980 (NCSM A2997).

Remarks.— The twisted distal zone is the chief diagnostic feature of *r. austrimontis,* but there are other differences from the nominate subspecies. It is larger in all dimensions than *r. rubromarginata,* though the two are virtually identical in somatic features. In general, gonopodal characters are less pronounced in *r. austrimontis,* and there is a tendency toward reduction of the flanges, prefemoral process, and length of the acropodite. In the nominate subspecies, the acropodite is more highly arched and the distal zone longer; likewise, the flanges are broader and the prefemoral process longer in this form. As indicated in the diagnoses, individuals of both subspecies display a bifurcate prefemoral process. However, in *r. rubromarginata* one component is always much longer than the other, whereas they are subequal in *r. austrimontis,* whose prefemoral process is generally short and stubby.

According to Stuckey (1965) the South Mountain range is a spur of the Blue Ridge which was segregated by the Catawba River. Evolution of *r. austrimontis* thus seems to be an example of speciation by geographic isolation. Full reproductive isolation does not appear to have been achieved since the configurations of the gonopods of forms along the Blue Ridge escarpment and the lowland western Piedmont are intermediate between those of the two subspecies. Hence, these specimens are considered intergrades and are discussed below.

Sigmoria rubromarginata intergrades Figs. 100-101, 134-135

Intergrade populations of *rubromarginata* occur in the Blue Ridge escarpment of western McDowell and eastern Buncombe counties, North Carolina, and range eastward to the vicinity of Morganton in the western Piedmont Plateau. A distributional hiatus of some 30 miles exists between the westernmost intergrade populations in eastern Buncombe County and the easternmost populations of the nominate subspecies in eastern Haywood County. The latter has not been collected in Buncombe County, and the situation in *rubromarginata* thus differs from those in *latior* and *nigrimontis,* where there are no such gaps. As shown in Figure 100, the distal zone of intergrades is turned slightly mediad, so that part of the face of the medial flange is visible in medial view. This condition and the degree of arch of the acropodite are approximately halfway between those of the two subspecies. The prefemoral processes, however, are typically reduced and more closely resemble those of *r. austrimontis.* Intergrade specimens were examined from the following localities:

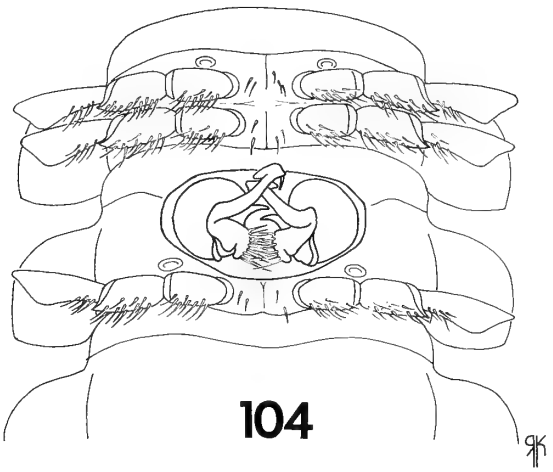
NORTH CAROLINA: *Buncombe Co.,* 3 mi. NE Fairview, along co. rd. 2785, 0.1 mi. S jct. co. rd. 2776, M, 9 September 1977 (NCSM A1717); 2.6 mi. S Black Mountain, along NC hwy. 9, 1.7 mi. N jct. co. rd. 2776, M, 12 July 1976 (NCSM A991); and E of Black Mountain, M, 3 August 1949, R.L. Hoffman (RLH). *McDowell Co.,* 2.8 mi. W Old Fort, along co. rd. 1400, 1.3 mi. W jct. co. rd. 1407, PNF, M, 20 August 1977, A.L. Braswell (NCSM A1627); 4.0 mi. SE Old Fort, along co. rd. 1131, 0.9 mi. E jct. co. rd. 1123, PNF, 5M, 5F, 15 September 1977 (NCSM A1746); 5.6 mi. SW Old Fort, along co. rd. 1100, 1.3 mi. W jct. co. rd. 1101, PNF, M, F, 15 September 1977 (NCSM A1749); 7.2 mi. NW Marion, along co. rd. 1436, 3.7 mi. N jct. NC hwy. 80, PNF, 3M, F, 23 May 1978 (NCSM A2017); 6.1 mi. NW Marion, along co. rd. 1436, 2.6 mi. E jct. NC hwy. 80, PNF, M, 24 May 1978 (NCSM A2019); 3.0 mi. NW Marion, along Buck Cr. at jct. US hwy. 70 and NC hwy. 80, PNF, M, F, 27 May 1979 (NCSM A2707); and 12.0 mi. SE Marion, along US hwy. 64, 0.4 mi. NE jct. NC hwy. 226, 5M, 3F, 7 May 1980 (NCSM A2999). *Burke Co.,* Morganton, 3M, 2F, date unknown, H.K. Morrison (RLH).

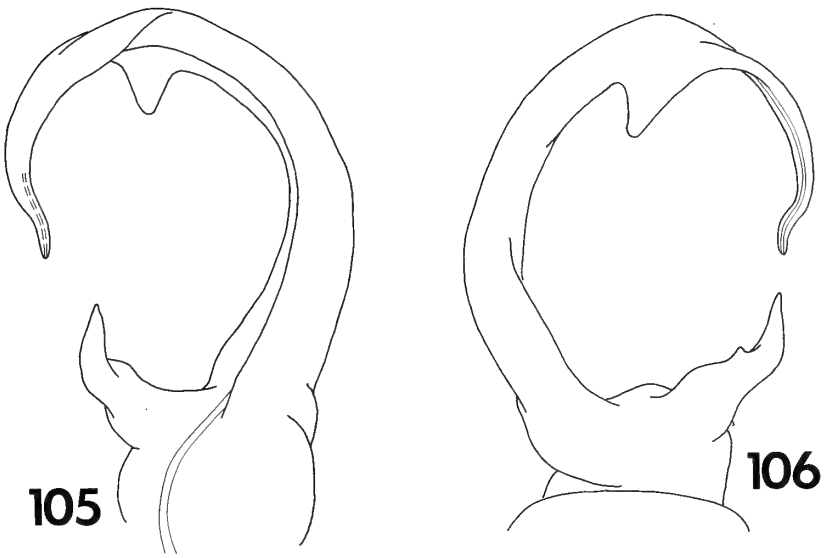
Sigmoria triangulata, new species Figs. 104-106, 134-135

Type specimens.— Male holotype (NCSM A658) and 2 male paratypes collected by R.M. Shelley and J.C. Clamp, 22 July 1975, from Madison Co., NC, 0.9 mi. N Hot Springs, along US highways 25-70, PNF. Male and female paratypes collected in PNF by same collectors on same date as follows: 5 males, 0.6 mi. N Hot Springs, along US highways 25-70; male and 2 females, 2.4 mi. E Hot Springs, along US highways 25-70, 0.7 mi. S junction of US Forest Service rd. #467; and 1 male and 1 female, 3.7 mi. NE Hot Springs, along US Forest Service rd. #467. Male paratypes deposited in FSCA and RLH.

Diagnosis.— A moderate-size species of *Sigmoria* with medial flange on distal zone and with red paranota and red metatergal stripes; gonopods with following diagnostic characters: arch high and rounded, shaped like ques-

tion mark, acropodite extending to level of prefemoral process; medial flange moderately long and narrow; lateral flange triangular, located on peak proximal to apical curve; distal zone extending dorsad from peak, bisinuately curved apically, directed toward prefemoral process.





FIGS. 104-106, *Sigmoria triangulata*. 104, gonopods *in situ*, ventral view of paratype. 105, telopodite of left gonopod of holotype, medial view. 106, the same, lateral view. Scale line for fig. 104 = 1.00 mm; line for other figs. = 1.00 mm for each.

Holotype.— Length 39.2 mm, maximum width 8.7 mm, W/L ratio 22.2%, depth/width ratio 60.9%. Segmental widths as follows:

collum	5.4 mm	9th-14th	8.5
2nd	7.0	15th	8.0
3rd	7.4	16th	7.8
4th	8.1	17th	6.8
5th-8th	8.7	18th	5.4

Color in life: paranota red; metaterga black with wide, red, transverse stripes along caudal edges connecting paranotal spots; collum with red stripes along both anterior and caudal margins.

Somatic features similar to *r. rubromarginata,* with following exceptions:

Width across genal apices 4.5 mm, interantennal isthmus 1.2 mm. Antennae reaching back only to just beyond caudal edge of 2nd tergite; relative lengths of antennomeres $2>5=6>4=3>1>7$. Facial setae as follows: epicranial and interantennal absent, frontal 1-1, genal 2-2, clypeal about 8-8, labral about 12-12, merging with clypeal series and continuing for short distance along genal border, about 4 setae on each side.

Dorsum smooth, polished, very little wrinkling. Collum very broad, extending well beyond ends of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 7, becoming blunt and progressively more acute thereafter.

Process of 4th sternum subsimilar to that of *r. rubromarginata,* consisting of two short, closely appressed, digitiform lobes, much shorter than width of adjacent coxae; knobs and elevated areas of 5th sternum similar to those of *r. rubromarginata,* distinct but much shorter than width of adjacent coxae; sternum of segment 6 convexly recessed between 7th legs to accommodate curvature of acropodites. Postgonopodal sterna glabrous, without lobes but with wide, shallow, central impressions. Coxal tubercles beginning on segment 10, low and blunt, becoming more pronounced on segments 14-16, and reduced thereafter.

Gonopodal aperture broadly ovoid, 3.4 mm wide and 1.7 mm long at midpoint, indented anteriolaterally, sides elevated above metazonal surface, caudal edge elevated and flared. Gonopods *in situ* (Fig. 104, of paratype) with acropodites crossing at distal extremity of peak, curving anteriad just beyond anteror margin of aperture. Gonopod structure as follows (Figs. 105-106): prefemoral process acuminate, bent sharply ventrad at midlength, directed toward peak of arch, with sharply pointed spur at bend, visible only in lateral view. Acropodite generally highly arched and rounded with one smoothly continuing curve, extending only to level of prefemoral process, divisions continuous and poorly defined; anterior bend broad, poorly defined, located at about 1/3 length; peak rounded, apex at midlength; apical curve broad, poorly defined, beginning about 2/3 length, smoothly continuing from apex of peak; distal zone long, extending in slight curve nearly straight downward (dorsad) from peak, not curving inward into arch, bisinuately curved apically; tip simple, acuminate, directed toward prefemoral process. Medial flange smaller than in *r. rubromarginata,* arising at beginning of apical curve, terminating at midlength of distal zone. Lateral flange broadly triangular, apex rounded, displaced proximad, located just distal to apex of peak, proximal to apical curve. Prostatic groove running along ridge on inner surface of acropodite, crossing to lateral side at apical curve.

Male paratypes.— The male paratypes agree closely with the holotype except that most lack the spur on the prefemoral process. The shape of the lateral flange is quite consistent, being subtriangular on all specimens and only slightly more pointed apically on a few individuals.

Female paratype.— Length 41.0 mm, maximum width 9.9 mm, W/L ratio 24.1%, depth/width ratio 67.7%. Agreeing essentially with holotype in somatic features except that collum not extending beyond edges of 2nd tergite.

Cyphopods with large receptacle, cupped around ventral end of valves, extending completely down lateral side of valves and halfway down medial, surface convoluted with deep folds and ridges. Valves moderate and subequal in size, surface finely granulate.

Variation.— The gonopods of *triangulata* are very uniform throughout its range. There are slight differences in the size of the lateral flange, and in some specimens it faces more dorsoventrally than laterally. Aside from this difference and that involving the prefemoral process mentioned under male paratypes, the gonopods of this species are virtually indistinguishable from each other.

Ecology.— *Sigmoria triangulata* is a cove dwelling species.

Distribution.— A small section straddling the North Carolina-Tennessee state line on the north side of the French Broad River in the Pisgah and Cherokee National Forests (Figs. 134-135). It can be roughly circumscribed by US highway 25-70, Tennessee highway 108, and Tennessee highway 70-North Carolina highway 208. Specimens were examined as follows:

NORTH CAROLINA: *Madison Co.,* 0.6 mi. N Hot Springs, along US hwy. 25-70, PNF, 5M, 22 July 1975 (NCSM A602, 633); 0.9 mi. N Hot Springs, along US hwy. 25-70, PNF, 3M, 22 July 1975 (NCSM A658) TYPE LOCALITY; 2.4 mi. W Hot Springs, along US hwy. 25-70, 0.7 mi. S jct. US For. Serv. rd. #467, PNF, M, 2F, 22 July 1975 (NCSM A657); 3.7 mi. NE Hot Springs, along US For. Serv. rd. #467, PNF, M, F, 22 July 1975 (NCSM A656); and vicinity of Hot Springs, PNF, 2M, F, 6 July 1968, R.L. Hoffman (RLH).

TENNESSEE: *Cocke Co.,* 13.7 mi. E Newport, Houston Valley Rec. Area along TN hwy. 107, CNF, 2M, 3F, 20 May 1978 (NCSM A1962); and 8.8 mi. E Newport, along co. rd. 2595, 0.9 mi. N ct. co. rd. 2486, CNF, 10 October 1978 (NCSM A2449). *Greene Co.,* 14 mi. S Greeneville, Paint Creek Rec. Area, 4 mi. NE Wolf Creek, CNF, M, F, 1 August 1962, R.L. Hoffman (RLH); and 10.5 mi. SE Greeneville, along 1st rd. N TN hwy. 70 W of NC state line, ca. 3 mi. N TN hwy. 70, CNF, M, F, 20 May 1978 (NCSM A1965).

Remarks.— *Sigmoria triangulata* is a very distinctive and easily recognizable species because of the triangular lateral flange. Although closely related to *rubromarginata,* the two are allopatric, as *triangulata* has never been collected south, and *rubromarginata* has never been encountered north of the French Broad River. Both occur close to the river in the vicinity of Hot Springs, but only on their respective sides.

The *Nigrimontis* Group

The *nigrimontis* group is comprised of two allopatric species, one of which, *nigrimontis,* is divided into four geographic races. This species ranges from the Black Mountains of Buncombe, Yancey, and McDowell counties, North Carolina, to Greene and Unicoi counties, Tennessee. The second species, *disjuncta,* occurs in the foothills and western Piedmont Plateau of Georgia and South Carolina, detached from the rest of the generic range. Both *nigrimontis nigrimontis* and *disjuncta* possess a short distal zone which terminates only a short distance below the level of the

peak, well above the prefemoral process. The tip is blunt and formed by an apical narrowing of both margins to a central termination. In *nigrimontis,* however, the length of the distal zone and the apical configuration grade smoothly into a wide variety of conditions, most of which are represented by the subspecies, *n. intermedia.* Likewise with other characters, such as the configurations of the medial and lateral flanges, the length of the peak, and the degree of arching of the acropodite, the condition in *n. nigrimontis* grades smoothly into those exhibited by the other subspecies. In general, the flanges of the *nigrimontis* group are smaller than those of the *rubromarginata* group, and in *disjuncta* and some populations of *n. intermedia,* the medial flange is vestigial and barely perceptible even in a "head on" view of the distal zone. The lateral flange of *n. intermedia* is variable but is always a clearly perceptible lamina on the stem of the acropodite; that of *disjuncta* is modified into a sharply pointed spine. *Sigmoria n. angulosa* and *disjuncta* possess an additional flange on the inner surface of the peak, and *n. unicoi* is distinguished by a lateral flange which is produced into a sharp apical point. *Sigmoria disjuncta* is also characterized by the course of the prostatic groove, which crosses to the lateral side on the prefemur and runs entirely along the lateral side of the acropodite. Basally the acropodites of *disjuncta, n. nigrimontis,* and *n. angulosa* are wide in alternating perpendicular planes, but this condition is indistinct in *n. intermedia* and *n. unicoi.*

Sigmoria nigrimontis (Chamberlin), new combination Figs. 134-135

Diagnosis.— A moderate-size species of *Sigmoria* with variable medial flange (often vestigial) on distal zone opposite lateral flange, and with red paranota and red metatergal stripes; gonopods highly variable but with following diagnostic characters: prefemoral process moderate to long, configuration variable; acropodite with regions poorly to well defined, arch extending to or beyond level of prefemoral process; basal zone widening in alternating perpendicular planes in some forms; peak flattened or gently curved; distal zone varying from short and terminating just below peak to long and extending to near level of prefemoral process; tip usually blunt, occasionally subacute, projecting dorsad from peak or bent sharply inward into arc; prostatic groove either running entirely along medial surface of acropodite or crossing to lateral side distal to anterior bend.

Ecology.— *Sigmoria nigrimontis* primarily inhabits coves, but it occasionally is found in other environments which will be described under the appropriate subspecies.

Remarks.— Because of the high variability of this species, it is very hard to diagnose on the basis of anatomical characters. It is best described in a

negative fashion as the species in North Carolina and Tennessee lacking a medial flange on the proximal portion of the peak which is neither *rubromarginata* nor *triangulata,* both of which are easily recognized. Chamberlin's name, *nigrimontis,* is retained as the specific name because it was proposed in 1947, one year earlier than Hoffman's name, *intermedia,* which now becomes the name for the race at Asheville. The other two subspecies, *n. angulosa,* in the mountains of the contiguous corner of Buncombe, Madison, and Yancey counties, North Carolina, and *n. unicoi,* in Unicoi County, Tennessee, are previously undescribed. These three populations, along with the nominate in the Black Mountains of Buncombe, Yancey, and McDowell counties, North Carolina, are the only ones showing morphological stability over a given area, and hence seem to warrant taxonomic recognition as subspecies. Populations in western Buncombe and Madison counties, North Carolina, and Greene County, Tennessee, are capriciously variable, with every known sample showing one or more differences from the others. These populations do not demonstrate sufficient consistency to be accorded a name, and, for the sake of convenience, are included under *n. intermedia.* The subspecies of *nigrimontis* can be distinguished as follows:

1. Distal zone short, terminating just below peak, well above level of prefemoral process; medial flange relatively short and broad, distinct (Fig. 108); Black Mountains of Buncombe, Yancey, and McDowell counties, North Carolina ..... *nigrimontis nigrimontis* (Chamberlin)

   Distal zone longer, extending well below peak, either bent inward into arch or projecting downward toward prefemoral process; medial flange relatively long and narrow 2

2. Peak with flange on inner surface, expanded into subtriangular lobe apically (Fig. 123); contiguous corners of Buncombe, Yancey, and Madison counties, North Carolina ..... *nigrimontis angulosa,* new subspecies

   Without this character 3

3. Distal zone bent sharply (90°) inward into arch near midlength (termination point of flanges); lateral flange relatively short and narrow, produced into sharp point apically, visible below bend of distal zone in medial view (Fig. 126); Unicoi County, Tennessee ..... *nigrimontis unicoi,* new subspecies

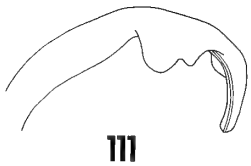
   Without these characters ..... *nigrimontis intermedia* (Hoffman)

Sigmoria nigrimontis nigrimontis (Chamberlin), new status

Figs. 107-112, 134-135

Deltotaria nigrimontis Chamberlin, 1947:28, figs. 11-12. Wray, 1967:151.
Sigiria nigrimontis: Chamberlin and Hoffman, 1958:48.

Type specimens.— Male and female paratypes (RVC) and another male paratype (AMNH) collected from Black Mountain, NC; collector and date(s) unknown. The holotype is missing from the AMNH (Type no. 1603), where Chamberlin (1947) and Chamberlin and Hoffman (1958)



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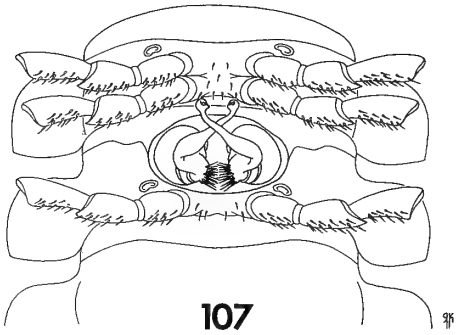

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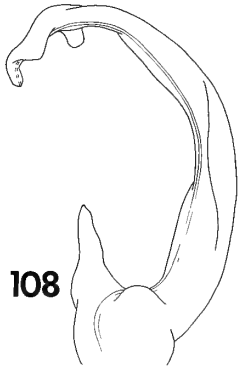

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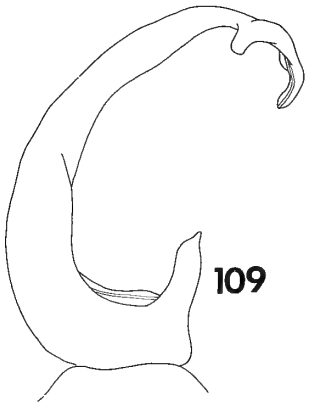

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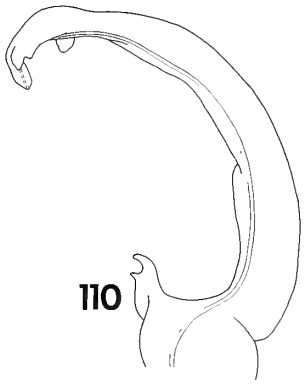

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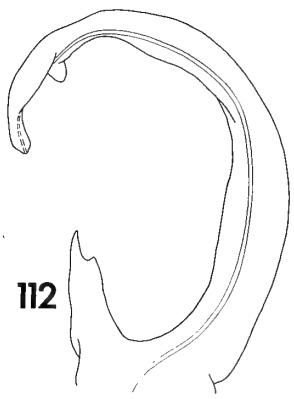


112

report its deposition. As stated in the Literature Review section, *nigrimontis* has never been authentically collected from the town of Black Mountain in Buncombe County, as reported by Chamberlin and Hoffman (1958), and I therefore believe that the citation of "Black Mountain" in the paratype vials and in the description (Chamberlin 1947) refers instead to an unknown locality in the Black Mountain range.

Diagnosis.— Characterized by the following combination of gonopodal characters: acropodite wide in alternating perpendicular planes from basal zone to middle of peak, arch a broad, continuous curve overhanging and extending slightly beyond level of prefemoral process, peak rounded, divisions poorly defined; distal zone relatively short; tip narrowing on both sides to blunt, central termination; medial flange located distal to lateral flange, usually relatively broad and conspicuous, rarely vestigal, with one or two lobes on margin; lateral flange always short and apically blunt or rounded, never long and narrow, located at apical curve.

Male paratype.— Length 42.3 mm, maximum width 8.3 mm, W/L ratio 19.6%, depth/width ratio 66.3%. Segmental widths as follows:

collum	6.6 mm	8th-10th	8.2
2nd	6.9	11th-13th	8.1
3rd	7.3	14th	7.9
4th	7.8	15th	7.7
5th	8.0	16th	6.9
6th-7th	8.3	17th	6.3
		18th	4.8

Color in life unknown, see comments under variation.

Somatic features similar to *r. rubromarginata,* with following exceptions:

Width across genal apices 4.2 mm, interantennal isthmus 1.7 mm. Antennae reaching back to caudal edge of 2nd tergite; relative lengths of antennomeres 2>3=6>5=4>1>7. Facial setae as follows: epicranial, interantennal, frontal, and genal not detected and apparently absent, clypeal about 6-6, labral about 12-12.

Dorsum smooth, polished, with only faint wrinkling. Collum broad, ends not extending beyond those of following tergite. Paranota strongly depressed, angled sharply ventrad; caudolateral corners blunt and rounded on all segments.

Process of 4th sternum very small, subsimilar to that of *r. rubromarginata;* knobs of segment 5 coalesced basally, flattened areas between posterior legs low but distinct; sternum of segment 6 convexly recessed between 7th legs to accommodate curvatures of acropodites.

FIGS. 107-112, *Sigmoria nigrimontis nigrimontis.* 107, gonopods *in situ,* ventral view of specimen from 13.4 mi. S Burnsville, Yancey Co., North Carolina. 108, telopodite of left gonopod of paratype, medial view. 109, the same, lateral view. 110, telopodite of left gonopod of another paratype, medial view. 111, distal part of acropodite of male from 9.6 mi. NW Marion, McDowell Co., North Carolina, lateral view. 112, telopodite of left gonopod of intergrade specimen from 4 mi. SE Barnardsville, Buncombe Co., North Carolina, medial view. Scale line for fig. 107 = 1.00 mm; line for other figs. = 0.56 mm for 108-109, 0.88 mm for 110-111, and 1.00 mm for 112.

Postgonopodal sterna flat, plate-like, with only shallow central impressions. Coxal tubercles low and blunt, becoming progressively sharper and more distinct posteriorly.

Gonopodal aperture broadly ovoid, 3.2 mm wide and 1.6 mm long at midpoint, sides raised and flared slightly. Gonopods *in situ* (Fig. 107, not this specimen) with acropodites crossing near midlengths of peaks, curving anteriad just beyond anterior margin of aperture. Gonopod structure as follows (Figs. 108-109): prefemoral process cuneate, tapering slightly apically, directed toward peak. Acropodite a broad, continuous curve, highly arched and rounded, overhanging and extending slightly beyond level of prefemoral process, divisions continuous and poorly defined, widening in alternating perpendicular planes from basal zone to peak; basal zone wide basally, narrowing distally in region of anterior bend; latter broad, poorly defined, continuous through peak with anterior bend; distal zone short, continuing broad curve of acropodite, bent abruptly inward into arch apically and directed toward prefemoral process; tip narrowing apically along both margins to blunt, central termination. Medial flange small, broadly triangular, located entirely on distal zone distal to lateral flange. Latter short, rounded, located in region of apical curve proximal to medial flange. Prostatic groove running along medial face of acropodite, crossing to lateral side at level of medial flange, opening terminally on distal zone.

Female paratypes.— All badly fragmented and unmeasurable. Agreeing with males in most structural details, except genae distinctly impressed medially.

Cyphopods with moderate receptacle, situated medial to valves, extending dorsad, not cupped over valves, surface slightly roughened.

Variation.— The prefemoral process displays a variety of shapes ranging from a small triangular wedge to the long cuneate structure on the paratype shown in Figures 108-109. However, the most common configuration is relatively short with a wide base and bifurcate tip, as shown by the AMNH paratype in Figure 110. The arch of the acropodite is reasonably constant, although it overhangs the prefemoral process more in some males. The medial flange, usually broadly triangular, has two lobes in some specimens (Fig. 110) and is vestigial in males from the range periphery (Fig. 112), a condition resembling that occurring in *n. intermedia.* The lateral flange, always proximal to the medial, is usually broad and apically rounded, but it has a second lobe in a male from McDowell County (Fig. 111) and is elongated in one from Stepps Gap, Yancey County.

Ecology.— The nominate subspecies primarily inhabits coves, but it also occurs in spruce-fir forests such as at the summit of Mt. Mitchell.

Distribution.— Black Mountain range of North Carolina, in southern Yancey County and the adjacent corners of Buncombe and McDowell counties (Fig. 134). As stated earlier, *nigrimontis* has never been authentically collected in the town of Black Mountain in Buncombe County. Material from this county was taken on the southern periphery of the Black Mountain range, well away from, and at a much higher elevation than, the town. Specimens were examined as follows: the types are omitted from the following list since their exact location is unknown.

NORTH CAROLINA: *Yancey Co.,* 4.7 mi. SE Micaville, along co. rd. 1169, M, 2F, 22 May 1978 (NCSM A1991); 10.3 mi. S Micaville, along US For. Serv. Rd. off NC hwy. 80, M, 23 May 1978 (NCSM A2002); 0.5 mi. down US For. Serv. rd. to Black Mtn. campground, off

Blue Ridge Parkway near milepost 350, M, 3 June 1974, R.L. Hoffman and L.S. Knight (RLH) and along waterfall trail, 12M, 6F, 10 July 1969, W.A. Shear (WAS); 2 mi. NW Black Mountain Campground, along trail to Mt. Mitchell, M, 2F, 11 July 1969, W.A. Shear (WAS); 13.4 mi. S Burnsville, along US For. Serv. rd., 2.3 mi. NW Blue Ridge Parkway, 3M, 20 July 1975 (NCSM A604); 14.4 mi. S Burnsville, along US For. Serv. rd., 1.6 mi. W Blue Ridge Parkway, 2M, F, 20 July 1975 (NCSM A665); along Blue Ridge Parkway below Pinnacle, 5,000′, 8M, F, 23 June 1951, L. Hubricht (RLH); Stepps Gap, Black Mtns., 6,000′, 3M, 2F, 26 June 1950, L. Hubricht (RLH); along Blue Ridge Parkway near jct. NC hwy. 128 to Mt. Mitchell, 4,200′, M, F, 23 May 1970, W.A. Shear (WAS); Mt. Mitchell, M, 25 June 1970, A.B. Gurney (NMNH); and Mt. Mitchell State Park, under logs at camping area, 2M, 1 August 1968, L.E. Bayless (WAS); fir forest camping area, M, 2 August 1968, L.E. Bayless (WAS), campground near summit, M, 31 July 1972, R.L. Hoffman (RLH), summit of Mt. Mitchell, 6,800′, 3M, 2F, 26 June 1950, L. Hubricht (RLH), F, 13 May 1970, F.A. Coyle (NCSM A2086), and 2M, 12 July 1955, A. Van Pelt (RLH). *McDowell Co.,* 7.8 mi. NW Marion, along co. rd. 1437, 0.5 mi. W jct. NC hwy. 80, 4M, 25 May 1978 (NCSM A2018); 9.6 mi. NW Marion, along US For. Serv. rd. off NC hwy. 80, 10M, 4F, 25 July 1975 (NCSM A662, A663); 4.6 mi. SW Little Switzerland, end of co. rd. 1443, 4.6 mi. W jct. NC hwy. 226A, past fish hatchery, 2M, 2F, 3 May 1978 (NCSM A2013); and along Blue Ridge Parkway, 1 mi. S Buck Creek Gap, M, 6F, 28 June 1951, L. Hubricht (RLH); *Buncombe Co.,* 4 mi. SE Barnardsville, along co. rd. 2173, 3.2 mi. E jct. co. rd. 2165, M, 2F, 6 September 1977 (NCSM A1708); and 4.1 mi. NNW Black Mountain (town), along co. rd. 2476 at Laurel Cr., 1.0 mi. NE North Fork Swannanoa River, 3M, 2F, 10 August 1978, R.E. and P.S. Ashton (NCSM A2394).

Remarks.— The characteristic widening of the basal zone in alternating perpendicular planes is also displayed by *truncata.* The ranges of the two millipeds are not very distant, but they do not seem closely related despite this common trait.

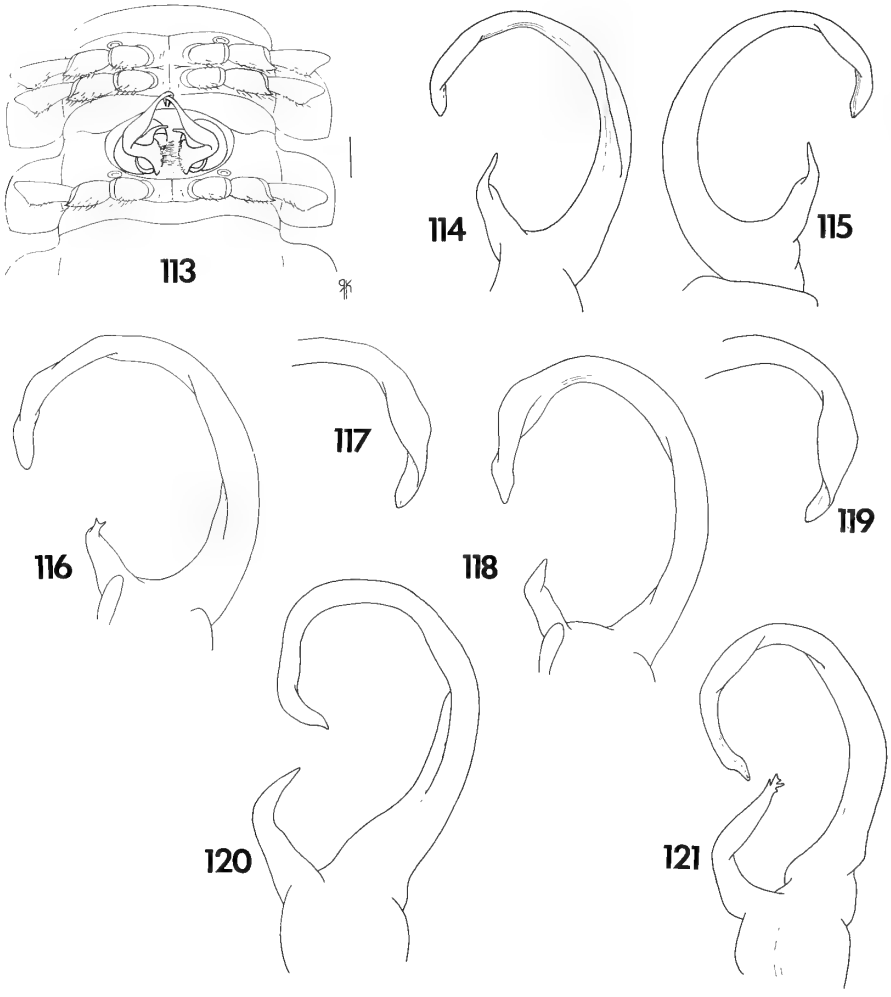
Intergrade specimens occur on the sides of the range of *n. nigrimontis* bordering *n. intermedia* and *n. angulosa.* These individuals have a longer distal zone, a smaller, sometimes vestigial medial flange, and a longer peak with a small flange on the inner surface. Unlike *rubromarginata,* there are no distributional gaps in the range of *nigrimontis,* and the subspecies are all connected by a cline of intermedial specimens.

Sigmoria nigrimontis intermedia (Hoffman), new combination, new status
Figs. 113-121, 134-135

Apheloria intermedia Hoffman, 1948a:346-348, figs. 1-2. Wray, 1967:151.
Sigiria intermedia: Chamberlin and Hoffman, 1958:48.

Type specimens.— Male holotype and female allotype (NMNH 1833) taken by unknown collector in July 1896, from Asheville, Buncombe Co., North Carolina. Hoffman (1948a) incorrectly stated that Asheville was in Ashe County and suggested that L.M. Underwood might have been the collector, since he is known to have collected in the Southeast in the summer of 1896. Male and female paratypes in RLH.

Diagnosis.— Characterized by following combination of gonopodal



FIGS. 113-121, *Sigmoria nigrimontis intermedia.* 113, gonopods *in situ,* ventral view of specimen from 6.4 mi. NE Asheville, Buncombe, Co., North Carolina. 114, telopodite of left gonopod of holotype, medial view. 115, the same, lateral view. 116, telopodite of left gonopod of another specimen from Asheville, medial view. 117, distal zone of acropodite of same gonopod, lateral view. 118, telopodite of left gonopod of specimen from 0.9 mi. SE Alexander, Buncombe Co., medial view. 119, distal zone of acropodite of same gonopod, lateral view. 120, telopodite of left gonopod of specimen from 9.2 mi. NW Burnsville, Yancey Co., North Carolina, medial view. 121, telopodite of left gonopod of specimen from 2 mi. W Flag Pond, Unicoi Co., Tennessee, medial view. Scale line for fig. 113 = 1.00 mm; line for other figs. = 1.00 mm for 114-119, 0.75 mm for 120-121.

characters: acropodite a broad, continuous, generally unmodified arch, extending to or slightly beyond level of prefemoral process; anterior bend and apical curve broad, poorly defined, continuous through peak; latter rounded, continuing curvature of anterior bend and apical curve; distal zone bent inward apically into arch to small but varying degrees; tip blunt or subacuminate. Medial flange usually vestigial and barely detectable, occasionally larger; lateral flange relatively long and narrow, margin smoothly continuous, arising at beginning of apical curve, terminating at midlength of distal zone.

Variation.— There is very little gonopodal stability to *n. intermedia,* and practically every sample is unique in some way. After five years of intensive collecting and study of this complex situation, the picture still is not clear. The material at hand shows a gradation of forms throughout the range, but does not reveal any localized units that can be considered separate subspecies. Consequently, I report trends of variation with the hope that future investigators, with more material from Madison and Yancey counties, North Carolina, will be able to provide a better analysis.

The logical beginning of this discussion is with the forms around Asheville, the type locality, which will retain the name *intermedia* should future studies indicate that nomenclatorial changes are warranted. The material under consideration was collected in July 1896 (male paratype) and September 1977 (male topotype). The latter specimen, which I collected, had a different texture to its dorsum and epicranium in that both were densely covered with finely raised granules located mainly in the midbody regions. The segments were glossy on the paranota. On the gonopods the male paratype (RLH) is identical to the holotype, and they undoubtedly came from the same locality within Asheville. Unfortunately, we do not know where this site was. The 1977 male was taken in a small cove on the northeast side of the city, along NC highway 694, 0.3 miles S of the junction of county road 2049. The configuration of its gonopods is very close to those of the holotype and paratype, but the prefemoral process is shorter and the lateral flange is broader though about the same length (Figs. 116-117). A male from 0.9 miles SE Alexander (RLH), which is near the present city limits of Asheville and, hence, a near topotype, differs considerably in that the prefemoral process is shorter still, the medial flange is distinctly visible, and the lateral flange is longer and narrower (Figs. 118-119).

Thus, even the forms around Asheville demonstrate considerable variation in the gonopod configuration. In general, however, these forms possess the simplest possible acropodite, which is merely a broadly curved blade with only a trace of flanges. Asheville also happens to be the southern and eastern limits of the range, as the race has not been taken in the Swannanoa

Valley or in the upper French Broad River basin. Proceeding west from Asheville, the male from near Alexander (Figs. 118-119) differs in having a medial flange, and this lamina is retained in specimens from Mars Hill, Madison County, which also has a larger lateral flange. In northeastern Buncombe and Yancey counties, northwest of Asheville, the medial flange is essentially absent, and the acropodite is basically a simple, broadly curved, unmodified blade (Fig. 120). However, the inward apical bend of the distal zone becomes progressively greater, and this continues into Greene and Unicoi counties, Tennessee. Accompanying this increased apical bending is an elongation of the prefemoral process, such that in Tennessee it extends beyond the level of the tip of the acropodite and has a number of terminal spurs (Fig. 121).

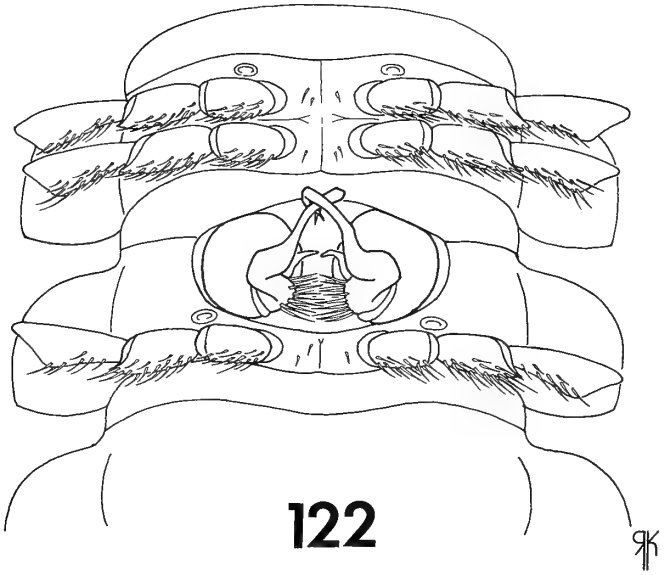
Ecology.— Sigmoria n. intermedia, while being a cove inhabitant, seems able to survive in deeper and wetter leaf piles than most of its congeners. I have collected it in wet leaves in seepage areas and in areas receiving direct spray from waterfalls.

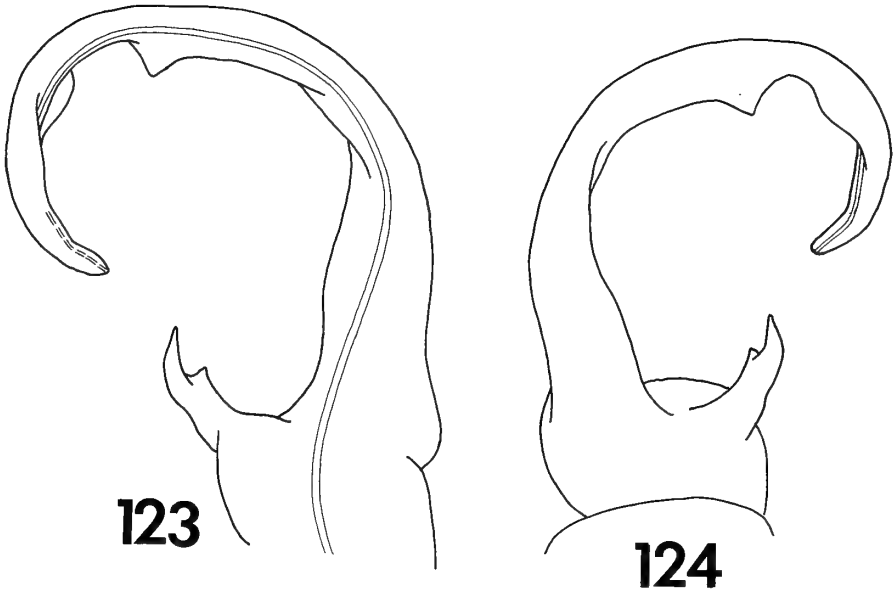
Distribution.— This race is the dominant form of *Sigmoria* north of the French Broad River. It occurs in the Blue Ridge Province roughly between the Nolichucky and French Broad Rivers, and ranges from Unicoi and eastern Greene counties, Tennessee, to the vicinities of Burnsville and Asheville, North Carolina (Figs. 134-135). Much of this area is in the Cherokee and Pisgah National Forests. The milliped has not been encountered east of the Blue Ridge Parkway and is absent from the Black Mountains in Yancey County. Specimens were examined as follows:

NORTH CAROLINA: *Buncombe Co.,* Asheville, 2M, 2F, July 1896, collector unknown (NMNH 1833, RLH) and Asheville, along NC hwy. 694, 0.3 mi. S jct. co. rd. 2049, M, 6 September 1977 (NCSM A1707) TYPE LOCALITY; 0.9 mi. SE Alexander, along US hwy. 70, M, F, 17 July 1961, R.L. Hoffman (RLH); 5.6 mi. E Weaverville, along co. rd. 2119, 0.9 mi. E jct. co. rd. 2116, M, 2F, 6 September 1977 (NCSM A1712); 6.4 mi. NE Asheville, 2nd jct. NC hwy. 694 and Blue Ridge Pkwy., 2M, F, 6 September 1977 (NCSM A1713); and 4.7 mi. E Barnardsville, along co. rd. 2173, 3.2 mi. E jct. co. rd. 2165, PNF, M, 6 September 1977 (NCSM A1709). *Yancey Co.,* 5.8 mi. WSW Burnsville, along co. rd. 1128, 0.1 mi. S jct. US hwy. 19, PNF, 3M, F, 20 July 1975 (NCSM A666). *Madison Co.,* 3.7 mi. NW Mars Hill, along co. rd. 1364, jct. co. rd. 1367, 2M, 11 September 1977 (NCSM A1731); 7.7 mi. NNW Mars Hill, along co. rd. 1318, jct. co. rd. 1341, PNF, M, 22 July 1975 (NCSM A389); ca. 9. mi. N. Mars Hill, along US hwy. 23 at Sams Gap, TN state line, 1,000′, PNF, 2M, 2 August 1962, R.L. Hoffman (RLH); and 13 mi. N Mars Hill, along NC hwy. 212, 2.5 mi. E TN state line, PNF, 3M, 4F, 20 May 1978 (NCSM A1967).

TENNESSEE: *Greene Co.,* 10.3 mi. E Greeneville, Horse Creek Rec. Area. CNF, M, 4F, 16 October 1978 (NCSM A2500). *Unicoi Co.,* 11 mi. SW Erwin, along co. rd. 2455, 8 mi. NE NC state line, CNF, 5M, 2F, 20 May 1978 (NCSM A1969).

Remarks.— *Sigmoria n. intermedia* has one of the simplest gonopods in the tribe Apheloriini; the acropodite is merely a smoothly rounded, continuous arch. A small lateral flange is the only constant structural





FIGS. 122-124, *Sigmoria nigrimontis angulosa*. 122, gonopods *in situ*, ventral view of paratype. 123, telopodite of left gonopod of holotype, medial view. 124, the same, lateral view. Scale line for fig. 122 = 1.00 mm; line for other figs. = 0.50 mm for each.

modification of its acropodite. It is therefore rather surprising to find such variability since there is so little structure on the gonopod that can change. However, the milliped blends changes in the length and shape of the prefemoral process with subtle variation in the curvature of the acropodite and in the size of the flanges to produce the most bewildering picture in *Sigmoria*. Local populations of *n. intermedia* doubtlessly gave rise to *n. angulosa* and *n. unicoi,* which continue the general trend of variation in their respective areas.

Sigmoria nigrimontis angulosa, new subspecies Figs. 122-124, 134-135

Type specimens.— Male holotype (NCSM A1727) and 3 male and 2 female paratypes collected by R.M. Shelley, 10 September 1977, from Yancey Co., NC, 6.8 mi. SW Burnsville, along NC highway 197, 3.0 mi. W junction with county road 1101, PNF. Male and female paratypes deposited in FSCA.

Diagnosis. — Characterized by flattened peak with long, narrow flange on inner surface, usually terminating in subtriangular lobe; arch overhanging and extending well beyond level of prefemoral process; distal zone relatively long, extending well below peak; lateral flange relatively long with margin slightly curved.

Variation. — Every gonopodal process or projection of *n. angulosa* varies in both size and shape. One male paratype lacks the spur on the prefemoral process, whereas the spur is so large in another that the process appears nearly bifurcate or U shaped. In the males closest to Barnardsville (RLH), the prefemoral process is long and acicular. The flange along the inner surface of the peak varies particularly in the terminal lobe, which is quite pronounced on some individuals. In one intergrade male from Yancey County (NCSM A1729), the flange is very narrow and barely perceptible. Its terminal lobe is nonexistent, and the flange is as wide apically as basally. The lateral flange is much larger on most males than on the holotype, and on some the edge is irregular. The general curvature of the acropodite is relatively consistent, although the peak is rounded in the aforementioned male from Yancey County. The bend of the distal zone also changes, being both sharper and straighter than the condition in the holotype.

Distribution. — South-central Yancey to northeastern Buncombe counties, North Carolina, in the middle of the range of *n. intermedia* (Fig. 134). The area lies south of US highway 19, west of the Craggy Mountains, and east of Barnardsville, and is bisected by state highway 197. In Yancey County the race occurs primarily in headwater areas of Cane Creek, a tributary of the North Toe River (Nolichucky drainage); in Buncombe County it is known only from the headwater region of Ivy Creek, a tributary of the French Broad River (Fig. 135). Specimens were examined as follows:

NORTH CAROLINA: *Buncombe Co.,* 5 mi. E Barnardsville, along NC hwy. 197, N side Craggy Mtns., 3,000′, PNF, 2M, 11 July 1969, R.L. Hoffman and L.S. Knight (RLH); 5.2 mi. E Barnardsville, along NC hwy. 197, 4.6 mi. W Yancey Co. line, PNF, M, 3F, 10 September 1977 (NCSM A1725); and 6 mi. E Barnardsville, along NC hwy. 197, 2.5 mi. W Yancey Co. line, PNF, M, 10 September 1977 (NCSM A1726). *Yancey Co.,* 8.4 mi. SW Burnsville, along co. rd. 1124, 3.7 mi. S jct. co. rd. 1126, PNF, M, F, 10 September 1977 (NCSM A1729); 6.8 mi. SW Burnsville, along NC hwy. 197, 3.0 mi. W jct. co. rd. 1101, PNF, 4M, 2F, 10 September 1977 (NCSM A1727) TYPE LOCALITY; vic. Pensacola, ca. 5 mi. S Burnsville, PNF, M, 18 June 1967, J.H. Hunt (FSCA); 8 mi. S Burnsville, along co. rd. 1100, 2.3 mi. S jct. NC hwy. 197, PNF, 2M, F, 10 September 1977 (NCSM A1728); and 7.6 mi. SE Burnsville, along co. rd. 1103, 0.2 mi. S jct. co. rd. 1102, PNF, M, 21 July 1975 (NCSM A432).

Remarks. — *Sigmoria n. angulosa* occurs entirely within the range of *n. intermedia,* but specimens that can be interpreted as intergrades occur on the periphery of its range, and the two are only subspecifically related. The diagnostic flange on the inner surface of the peak appears to be a specialization; it is also found in *disjuncta.* This structure is not homologous to the medial flange on the proximal portion of the peak found in other species of *Sigmoria.* The specific name refers to the many surfaces, and hence angles, formed by the flanges, lobes, and the alternately wide and narrow basal zone. One unusual feature of *n. angulosa* is its occurrence across a mountain divide between two different river systems, something that few montane "sigmoid" xystodesmids have achieved. *Sigmoria translineata* is one notable exception, as it occurs on both sides of the high divide along the North Carolina-Tennessee state line in the Great Smoky Mountains National Park, where the peaks are around 5-6,000 feet.

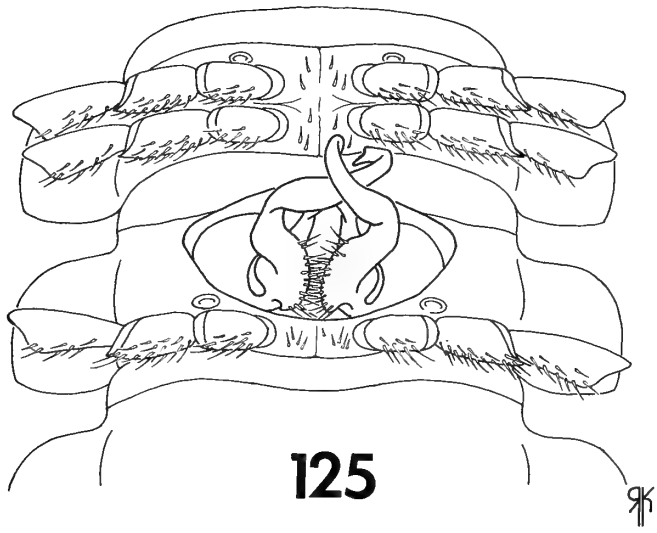
Sigmoria nigrimontis unicoi, new subspecies Figs. 125-127, 134-135

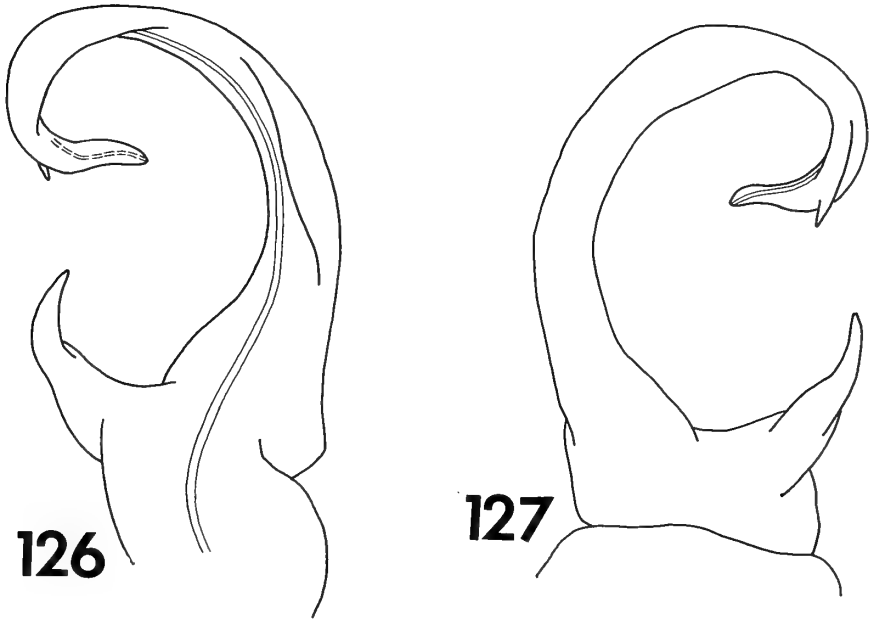
Type specimens. — Male holotype (NCSM A1970) and 3 female paratypes collected by R.M. Shelley and W.B. Jones, 20 May 1978, from Unicoi Co., TN, 6.8 mi. SW Erwin, along Tennessee highway 81, 0.5 mi. S junction with US highway 19W, CNF. Two male and 1 female paratypes (RLHO collected by R.L. Hoffman and L.S. Knight, 2 August 1971, from Unaka Springs, Unicoi Co., also in the CNF. Female paratype deposited in FSCA.

Diagnosis. — Characterized by flattened peak; distal zone bent sharply (90°) inward into arch at midlength; medial flange long and narrow, arising at midlength of peak, terminating proximal to bend of distal zone; lateral flange very narrow, terminating in sharply pointed spur at bend of distal zone, visible in medial view.

Variation. — The two male paratypes from Unaka Springs agree closely with the holotype, except that the spur on the lateral flange is larger and more pronounced.

Distribution. — Known only from Unicoi County, Tennessee, south of





FIGS. 125-127, *Sigmoria nigrimontis unicoi*. 125, gonopods *in situ*, ventral view of paratype. 126, telopodite of left gonopod of holotype, medial view. 127, the same, lateral view. Scale line for fig. 125 = 1.00 mm; line for other figs. = 1.00 mm for each.

the Nolichucky River. Unaka Springs is on the south bank of the Nolichucky River, and I have searched in vain for the milliped in cove habitat north of the River in and near Erwin. Thus, the Nolichucky River appears to be the northern range limit for the subspecies. Specimens were examined as follows:

TENNESSEE: *Unicoi Co.,* 6.8 mi. SW Erwin, along TN hwy. 81, 0.5 mi. S jct. US hwy. 19W, CNF, M, 3F, 20 May 1978 (NCSM A1970) TYPE LOCALITY; and Unaka Springs, ca. 2.6 mi. S Erwin, CNF, 2M, F, 2 August 1971, R.L. Hoffman and L.S. Knight (RLH).

Remarks. — As with *n. angulosa, n. unicoi* represents a local population of *n. intermedia* that has achieved more stability than most such populations. More material of *n. unicoi* is needed, however, and future field efforts should focus on western Unicoi County and the CNF in the adjacent southeastern corner of Washington County. A field trip to the latter area in 1978 was unproductive, but it still seems likely that *n. unicoi* occurs there. The milliped should also be expected in the Unicoi Wildlife Management Area.

Sigmoria disjuncta, new species Figs. 128-130, 137-138

Type specimens. — Male holotype (NCSM A2059) and 4 male and 2 female paratypes collected by R.M. Shelley and W.B. Jones, 9 June 1968, from Oconee Co., SC, 2.3 mi. NW Mountain Rest, along SC hwy. 28, 4.8 mi. N junction of SC hwy. 258, in the Sumter National Forest. Male paratype deposited in FSCA.

Diagnosis. — A moderate-size species of *Sigmoria* with vestigial medial flange on distal zone and with purple-gray paranota and metatergal stripes; gonopods with following diagnostic characters: prefemoral process and lateral flange spiniform, latter located nearly opposite vestigial medial flange in apical curve region; acropodite with regions poorly defined, leaning over and extending well beyond level of prefemoral process; without rounded or flattened arch; peak rising to apex distally, with flange on inner margin proximally, terminating in subtriangular lobe at about 2/3 length; distal zone not coplanar with other regions of acropodite, projecting sublaterad from peak; prostatic groove crossing to lateral side on prefemur, running entirely along lateral surface of acropodite.

Holotype. — Length 36.8 mm, maximum width 9.3 mm, W/L ratio 25.3%, depth/width ratio 62.4%. Segmental widths as follows:

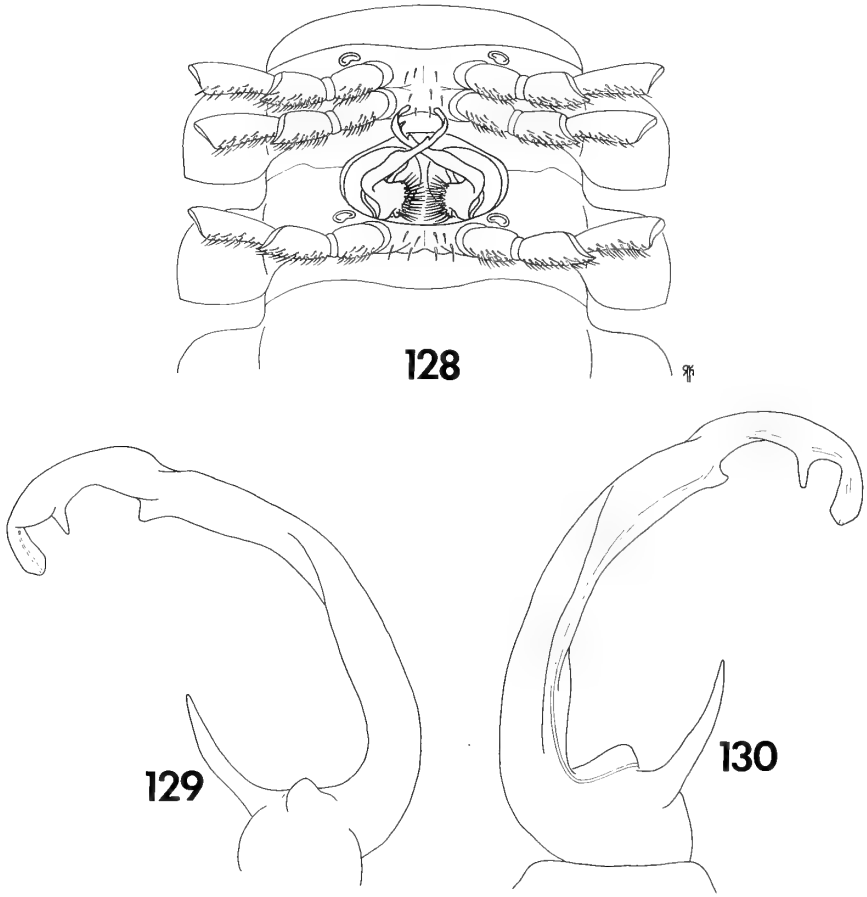
collum	6.9 mm	14th	9.1
2nd	7.4	15th	8.9
3rd	8.2	16th	8.2
4th	8.7	17th	7.2
5th-7th	9.1	18th	5.2
6th-13th	9.3		

Color in life: paranota purple-gray, metaterga black with purple-gray stripes along caudal edges connecting paranotal spots, collum with purple-gray stripes along both anterior and caudal edges.

Somatic features similar to *r. rubromarginata,* with following exceptions:

Width across genal apices 4.6 mm, interantennal isthmus 1.4 mm. Antennae reaching back to caudal edge of 3rd tergite; relative lengths of antennomeres 2>3>6=5=4>1>7. Facial setae as follows: epicranial, interantennal, frontal, and genal absent, clypeal about 13-13, labral about 18-18.

Dorsum smooth, slightly coriaceous on paranota. Collum broad, ends extending slightly beyond those of following tergite. Paranota strongly depressed, angled sharply ventrad, caudolateral corners rounded through segment 6, becoming progressively more pointed thereafter.



FIGS. 128-130, *Sigmoria disjuncta.* 128, gonopods *in situ,* ventral view of paratype. 129, telopodite of left gonopod of holotype, medial view. 130, the same, lateral view. Scale line for fig. 128 = 1.00 mm; line for other figs. = 1.00 mm for each.

Process of 4th sternum slightly larger than that of *r. rubromarginata,* but still shorter than widths of adjacent coxae; knobs and flattened areas of 5th sternum likewise more distinct than those of *r. rubromarginata;* 6th sternum convexly recessed between 7th legs to accommodate curvatures of acropodites, 7th legs set slightly farther apart than 6th. Postgonopodal sterna flattened, plate-like, beginning on segment 8, low and blunt through segment 9, becoming progressively sharper and more pointed posteriorly.

Gonopodal aperture ovoid, 3.4 mm wide and 1.7 mm long at midpoint, indented anteriolaterally, sides flush with metazonal surface. Gonopods *in situ* (Fig. 128, of paratype) with acropodites crossing near midlengths of peaks, curving anteriad beyond anterior margin of aperture and projecting between 7th legs. Gonopod structure as follows (Figs. 129-130): prefemoral process a long, spiniform structure, directed toward apical curve of acropodite. Acropodite without definite arch configuration of congeners, leaning over and extending well beyond level of prefemoral process, regions poorly defined and indistinguishable, widening in alternating perpendicular planes for proximal 1/3 of length; basal zone bent sharply anteriad basally; anterior bend poorly defined; peak long, about 1/3 of acropodite length, rising to apex distally, with narrow, laterally directed flange along inner edge, arising distal to anterior bend, terminating in subtriangular lobe on distal 1/3 of peak; apical curve broad, poorly defined; distal zone bent sharply at midlength, projecting sublaterad from peak, not coplanar with rest of acropodite; tip narrowing apically along both margins to blunt, central termination. Medial flange vestigial, long and narrow, located on distal zone between lateral flange and bend of distal zone. Lateral flange modified into moderately sharp spine, situated on inner margin of acropodite, directed toward prefemoral process. Prostatic groove crossing to lateral side of telopodite on prefemur, running entirely along lateral side of acropodite, opening terminally on distal zone.

Male paratypes. — The male paratypes agree closely with the holotype in all structural details.

Female paratype. — Length 37.9 mm, maximum width 9.6 mm, W/L ratio 25.3%, depth/width ratio 70.8%. Agreeing closely with male in somatic features, except paranota more strongly depressed, giving appearance of more highly arched body.

Receptacle large, hoodlike, cupped around ventral end of valves, extending about 2/3 of way down both sides, surface coriaceous. Valves moderate, subequal, surface coriaceous.

Variation. — Except for the prefemoral process, the gonopods of the available specimens of *disjuncta* agree closely with one another. The prefemoral process is always spiniform, but its length varies and it is slightly curved in the male from Toccoa Falls. In the males from Dawson County, Georgia, the structure is much shorter, being about half as long as the condition in the holotype.

Ecology. — *Sigmoria disjuncta* does not seem to be a cove dwelling species. Both times I collected it, the millipeds were taken well away from the nearest streams, in hardwood leaves and humus. In Hall County, Georgia, the species was found on a steep bank leading down to a stream, some 40-50 feet above the water and its associated rhododendrons.

Distribution. — Blue Ridge escarpment and the adjacent foothills of the western Piedmont Plateau of northeastern Georgia and southwestern South Carolina (Figs. 137-138). Specimens were examined as follows:

SOUTH CAROLINA. — *Oconee Co.,* 2.3 mi. NW Mountain Rest, along SC hwy. 28, 2.3 mi. N jct. SC hwy. 258, Sumter National Forest, 4M, 2F, 9 June 1978 (NCSM A2059) TYPE LOCALITY.

GEORGIA. — *Stephens Co.,* Toccoa Falls, 2 mi. NW Toccoa, Chattahoochee National Forest, 4F, 17 April 1961, L. Hubricht (RLH) and M, 4 July 1963, R.L. Hoffman (RLH). *Hall Co.,* along GA hwy. 52, 2.8 mi. N jct. US hwy. 23 in Lula, 2M, F, 29 April 1979 (NCSM A2604). *Dawson Co.,* wooded slope 6 mi. SW Dawsonville, 2M, 8 April 1961, L. Hubricht (RLH).

Remarks. — *Sigmoria disjuncta* is unique in several ways. It is the only species whose range is not known to be attached to the rest of the generic range (Fig. 131). The purple-gray paranota and metatergal stripe color pattern of *disjuncta,* shared with *stenogen,* permits reliable field identification, since *disjuncta* is the only xystodesmid in its range with this pattern. On the gonopods, the spiniform prefemoral process and lateral flange, and the lack of an arch to the acropodite, are all diagnostic for *disjuncta,* as is the course of the prostatic groove, which crosses to the lateral side on the prefemur rather than at the medial flange or anterior bend, and runs entirely along the lateral surface of the acropodite. The distal zone of *disjuncta* is not coplanar with the basal zone and the rest of the acropodite, but instead projects sublaterad, although two-dimensional drawings from medial and lateral views show it directed toward the prefemoral process.

The allopatric distribution of *disjuncta* suggests that it is a relict from a time when the *nigrimontis* group occupied a much larger range, possibly occurring well into the Piedmont Plateau. Such a distribution is obtained in a number of plant species (Hardin and Cooper 1967) and in the milliped, *Delophon georgianum* Chamberlin (Shelley 1979b, Filka and Shelley 1980a). In the latter case, a disjunct population occurs in the Kings Mountain region detached from the bulk of the diplopod's range in the Blue Ridge Province. The unique gonopodal features of *disjuncta* suggest a lengthy period of isolation from the rest of the *nigrimontis* group, and its ecological preference for climax deciduous forests as opposed to rhododendron coves may have been an important factor in its evolution.

Ecology

Except for *latior* and *areolata,* the species of *Sigmoria* occurring in the mountains inhabit essentially the same environment — cool, moist coves or similar sites along streams. They prefer places with rushing water, particularly where there is a small waterfall or cataract, and are typically found under thin layers of leaves on relatively hard substrates on river banks. Thick leaf piles and matted litter are avoided, and the animals rarely occur under large rocks, decaying logs, or bark of decaying logs. Shade is essential; the millipeds avoid open clearings with direct sunlight even if other parameters of the site are favorable. Rhododendron is usually present in

these coves and serves as an indicator of "sigmoid" diplopod sites, since other apheloriine genera occupy the same biotope. The forms are not microsympatric, however, and I know of no place inhabited by more than one "sigmoid" species. Except for *truncata,* the millipeds generally shun rhododendron litter but are usually found nearby under associated hardwood species such as dogwood and red maple. A dense rhododendron thicket is thus unlikely to contain these millipeds as is a climax hardwood forest on a hillside, which would be a likely habitat for *Apheloria* and *Cherokia.*

One of the best places to find cove habitat is on the inside of hairpin curves on mountain roads. Water is frequently present at these locations, and there is often a waterfall and a trail leading into the forest. A few scrapes in the litter along the edge of the trail or in that on the banks of the stream will usually produce several brightly striped xystodesmids. Excursions deep into the forest are unnecessary and have a low probability of success. These hairpin turn locations have the added benefit of easy access, since there is often a gravel pull-off spot for cars. Consequently, to collect *Sigmoria* or any other "sigmoid" xystodesmid, I select an area from which specimens are needed and drive along the roads stopping only at sites with these characteristics, either coves or accessible river bottoms. With a bit of practice, one can become adept at site selection and find specimens at a high percentage of the localities investigated.

The other two montane species, *latior* and *areolata,* have less specialized habitat requirements and inhabit predominantly deciduous forests such as occur on most hillsides. This preference for a more continuous and widespread habitat partly explains the success of *latior* in colonizing such a large area in the mountains and lowlands while other montane species are restricted to small ranges in the Blue Ridge Province. It also seems to explain the absence of nearly all the other upland species from mountains north of the Toe-Nolichucky River. These mountains are more distinct and separate, and there are fewer ridges and clusters of peaks than in the dense ranges of Buncombe County and the Smokies. Consequently, cove habitats are rarer in these northern mountains, and the forms requiring this environment are thus absent from southern Virginia and northeastern North Carolina. Since *latior* can live in most mesic deciduous forests, it thrives in the northern mountains and has spread into the Ridge and Valley Province of Virginia and the Alleghany Mountains of southern West Virginia.

Five species of *Sigmoria* occur east of the mountains in the Piedmont Plateau and Coastal Plain: *latior* and *stenoloba* in North Carolina; *latior, quadrata,* and *laticurvosa* in South Carolina; and *disjuncta* in South Carolina and Georgia. The first two occur sympatrically in the foothills and western Piedmont of Wilkes and Catawba counties, where they are found

under rocks, logs, and in litter and humus layers of predominately hardwood localities. However, they inhabit markedly different environments in this region. *Sigmoria stenoloba* occurs in marginal hardwood localities that are disturbed, contain considerable pine, are relatively xeric, or are in some way inferior to the mesic climax forests which *latior* inhabits. The latter sometimes occurs in substandard habitats in eastern Piedmont North Carolina where tracts of climax forest are scattered, but I have never encountered it in places that are as ostensibly undesirable as those *stenoloba* inhabits.

Habitat in the Piedmont of South Carolina is much less favorable than in the North Carolina Piedmont due to the larger number of cotton farms which are reverting back to forests and are currently in pine stages of succession. Hardwood tracts suitable for xystodesmids are largely restricted to areas near water sources; hence most of these xystodesmids have been collected along banks of streams, also under thin layers of leaves on relatively hard substrates. As with all xystodesmids they shun beech litter and seem to prefer that of dogwoods, maples, or oaks. In mixed pine-hardwood localities these species may be encountered in leaf piles instead, which are the best spots available in these particular environments. *Sigmoria latior* is the only species that has invaded the Coastal Plain, and it has spread to the edge of the Atlantic Ocean in Charleston-Colleton counties, South Carolina. It occurs in deciduous forests, in a variety of miscellaneous habitats (enumerated by Shelley 1976), and in cypress swamps, where I have found specimens under thin layers of leaves on hard substrates, often in association with *Pachydesmus crassicutis incursus* Chamberlin.

Two points in this ecological discussion bear elaboration. The first is the preference of most species of *Sigmoria* and other "sigmoid" xystodesmids for thin layers of leaves on relatively hard substrates near water sources. Aside from *latior, stenoloba, areolata,* and *disjuncta* species of *Sigmoria* will rarely be found far from water or in humus, thick piles of leaves, or under logs. They occupy a distinct and readily definable microhabitat which differs markedly from that occupied by *Apheloria, Cherokia,* and a number of other apheloriine and rhysodesmine genera.

The second and more important point is that only one species of *Sigmoria* exists at any one site; i.e. they are not microsympatric. This is true of every habitat occupied by these millipeds in the mountains, Piedmont, or Coastal Plain. Another species with overlapping range may occur a few miles away beside another creek or in another valley, but I have never collected two at a site, and there are no samples containing two or more species in any museum or private collection. Subtle but distinct habitat differences explain why *stenoloba* and *latior* do not coexist, but I detect no consistent differences between the mountain coves or South Carolina Piedmont en-

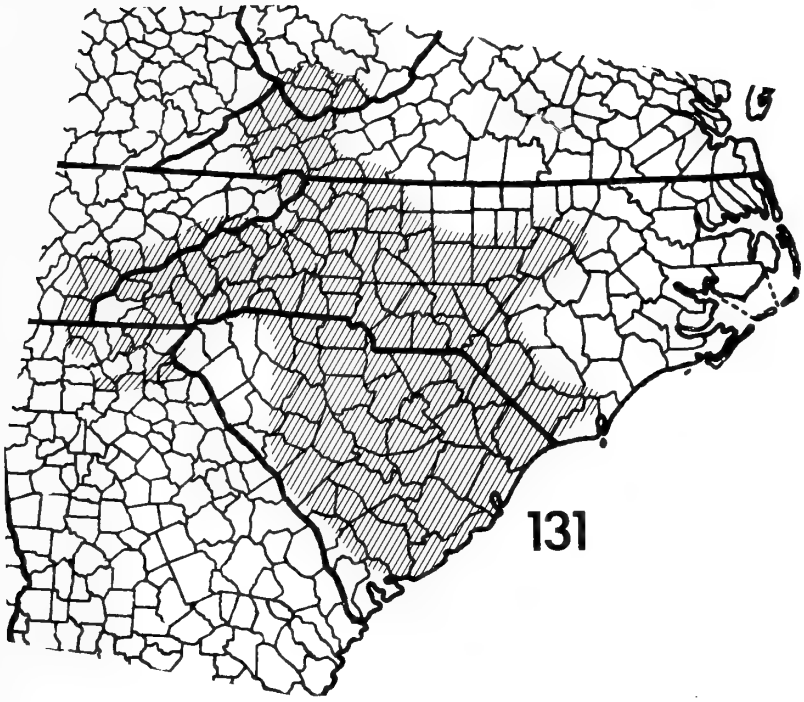


FIG. 131, Distribution of *Sigmoria*.

vironments. They appear to be similar enough that the reason for this phenomenon is probably competition rather than features of the locality. The millipeds appear to have nearly identical ecological requirements and may occupy essentially the same niche. Thus, they probably obey the competitive exclusion principle, sometimes referred to as Gause's theorem, which says, "Two species cannot indefinitely coexist in the same locality if they have identical ecological requirements" (Mayr 1970).

DISTRIBUTION

Sigmoria is the dominant "sigmoid" xystodesmid milliped genus in the Blue Ridge Province of eastern Tennessee and western North Carolina, and is most diverse between the Nolichucky and Little Tennessee rivers. Centers of abundance are the French Broad River Basin and the Great Smoky Mountains, with seven species each. Hoffman (1950a) and Chamberlin and Hoffman (1958) reported that *Sigmoria* occurred in the southern Appalachians from central West Virginia to western South Carolina, central Tennessee, and eastern Texas, but these range statements have changed

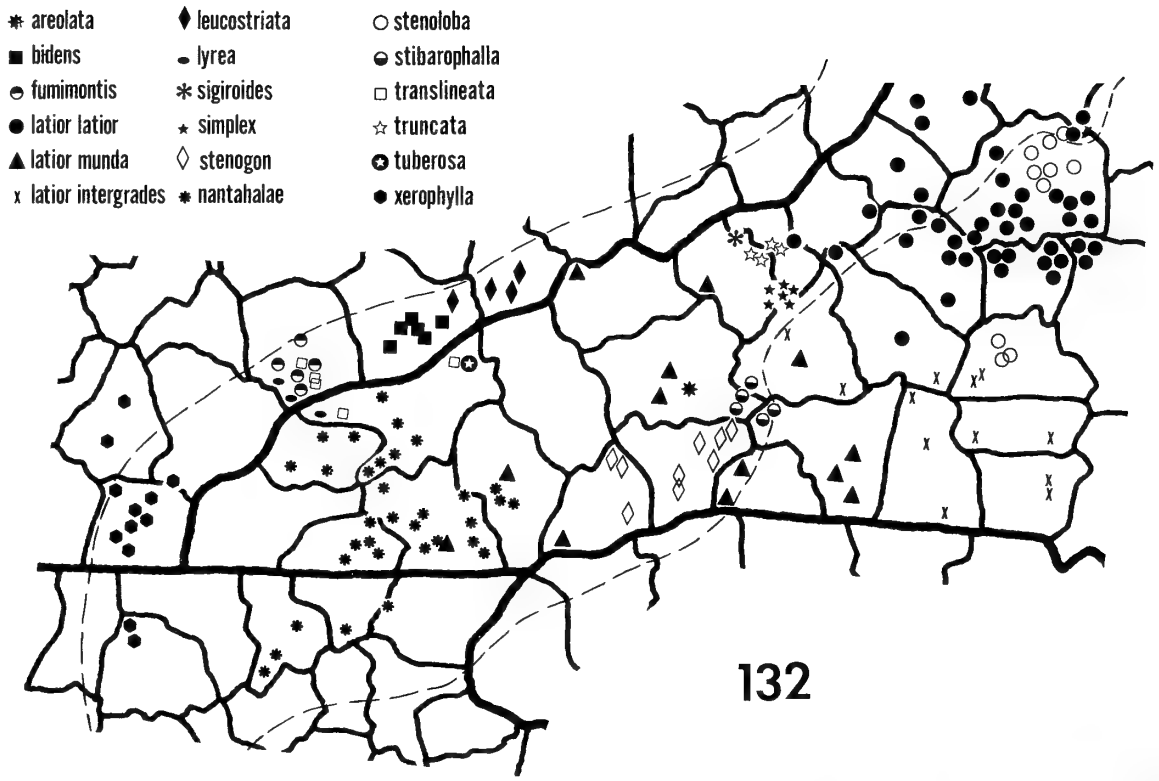


FIG. 132, Distribution by counties of species and subspecies of the *latior, simplex, stenogon, translineata, bidens, leucostriata,* and *tuberosa* groups in western North Carolina, eastern Tennessee, and northern Georgia. The dashed line in this and other maps shows approximate limits of the Blue Ridge Physiographic Province.

along with the composition of the genus. Removal of *mimetica* and *houstoni* from *Sigmoria* eliminates the last two areas, and the one remaining can now be defined more inclusively.

The distribution of *Sigmoria* is depicted in Figure 131, in which a smooth curve has been drawn around known range extremes in all directions. Spot maps of species distributions by counties and by river basins in western North Carolina, eastern Tennessee, and northern Georgia are presented in Figures 132-135. *Sigmoria* thus spans five physiographic provinces in six states, and ranges from the mountains of southern West Virginia, in the north, to the Coastal Plain of southeastern South Carolina, in the south. It occurs west to the edge of the Blue Ridge Province in eastern Tennessee and south to the edge of the Piedmont Plateau in northern Georgia. Eastward, *Sigmoria* extends to about 30 miles from the Atlantic Ocean in Brunswick County, North Carolina, and Horry County, South Carolina, and occurs nearly to the high tide mark at Edisto Beach State Park, Charleston-Colleton counties, in the latter state. Most of South Carolina is occupied; the only places where *Sigmoria* has not been collected in this state are the southern tip and the western corner, except for the extreme western fringe

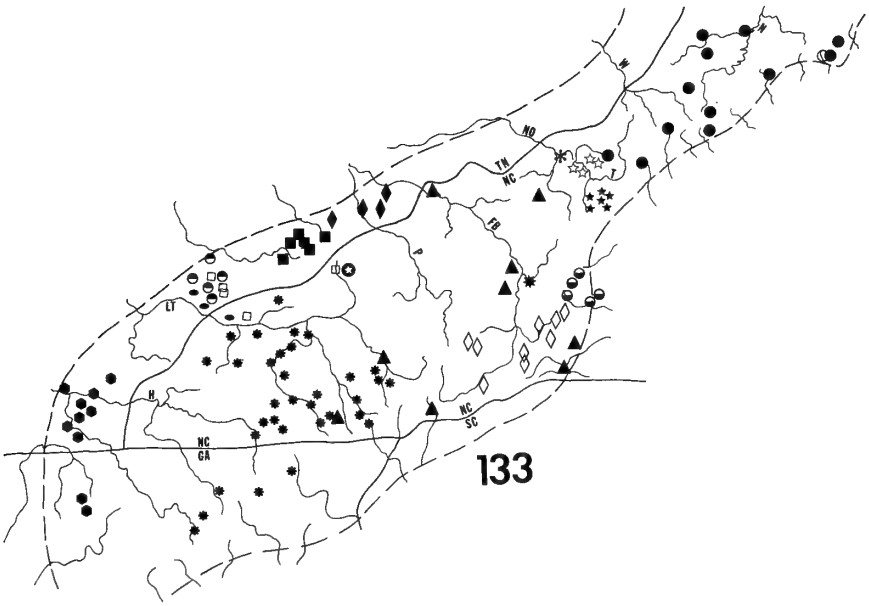


FIG. 133, Distribution by river basins in the Blue Ridge Province of species and subspecies of the same species groups shown in Fig. 132. Symbols as shown in Fig. 132; river abbreviations as follows: FB, French Broad; H, Hiwassee; LT, Little Tennessee; N, New; NO, Nolichucky; P, Pigeon; T, Toe; W, Watauga.

around the Chattooga River in Oconee County, where *disjuncta* occurs. The distributions in North Carolina and, to a lesser extent, Virginia, are irregular due to range disparities of *latior,* as discussed in a subsequent paragraph.

Seven species of *Sigmoria* occur in the GSMNP (Fig. 136). The nominate subspecies of *rubromarginata* is the dominant form in the northern section of the Park north of US highway 441, and it is particularly abundant in the Cosby Picnic Area. Most species, however, occur in the southern section of the Park on the Tennessee side. *Sigmoria bidens* is common around Gatlinburg, ranging from the Roaring Fork Nature Trail to Elkmont, and eastward along US highway 441 to the point where it starts climbing to Newfound Gap. All three species of the *translineata* group occur in Blount County and are apparently absent from Sevier County. Two of these, *translineata* and *lyrea,* occur across the state line in the Swain County, North Carolina, portion of the Park, and the former ranges to the Collins Creek Picnic Area, along US highway 441 in the Oconaluftee Valley. The dominant species in this valley, however, is *tuberosa,* which extends from Cherokee, outside the Park, to the point where the highway begins climbing to the eastern side of Newfound Gap. The nominate subspecies of *rubromarginata* is the only form occurring in the Haywood County, North Carolina, section of the Park, and it ranges south to Deep Creek near Bryson City. The only species collected in the Forney Creek area south of Bryson City is *nantahalae.* This is an important discovery because it is the first record of *nantahalae* both from the Park and from north of the Little

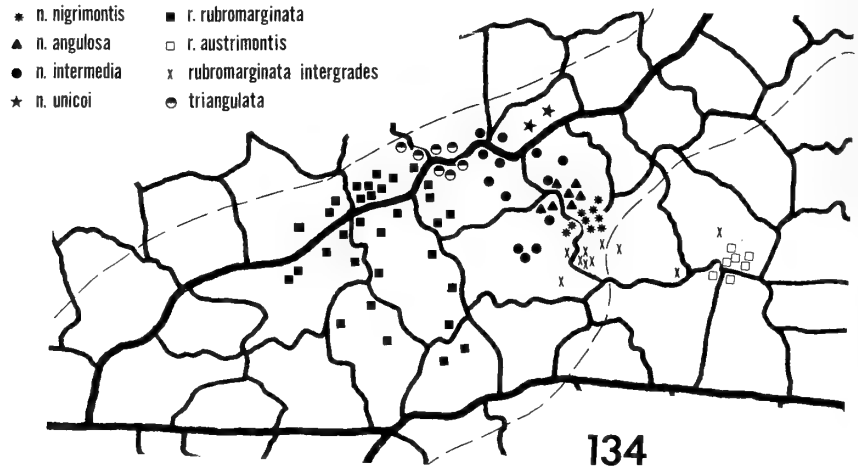


FIG. 134, Distribution by counties of species and subspecies of the *rubromarginata* and *nigrimontis* groups in western North Carolina and eastern Tennessee.

Tennessee River. Five species in the Park — *translineata, lyrea, fumimontis, bidens,* and *tuberosa* — have the red paranota-blue metatergal stripe color pattern, and *xerophylla,* in Tennessee mountains south of the Park, also exhibits these colors. The distribution of this pattern in *Sigmoria* is therefore restricted to the southwestern part of the generic range, where two sympatric species in an undiagnosed apheloriine genus also display it. This color pattern may have some ecological basis and thus be convergent in separate lineages, or it may represent an ancestral condition.

The distributions of species and subspecies of *Sigmoria* in South Carolina and Georgia are shown in Figures 137-138. Three lineages — the *latior, quadrata,* and *nigrimontis* groups — occur in South Carolina (Fig. 137), and the first, represented by *l. hoffmani* and *latior* intergrades, is most abundant. The last two groups are restricted to a small rectangular area south of Columbia and the western fringe of Oconee County, respectively. Three lineages — the *stenogon, leucostriata,* and *nigrimontis* groups — also occur in Georgia (Fig. 138), but only in a small section of the mountains and adjacent edge of the Piedmont in the northern part of the state.

An updated range map for *Sigmoria latior,* including localities in my 1976 paper and new ones cited herein, is presented in Figure 139. The central in-

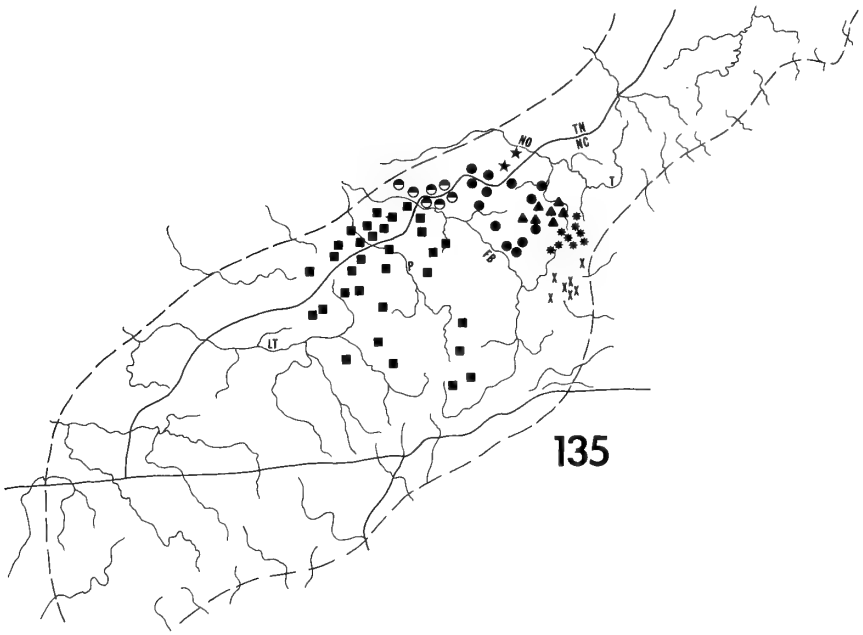


FIG. 135, Distribution by river basins in the Blue Ridge Province of the same species groups shown in Fig. 134. Symbols as shown in Fig. 134; river abbreviations as follows: FB, French Broad; LT, Little Tennessee; P, Pigeon; NO, Nolichucky; T, Toe.

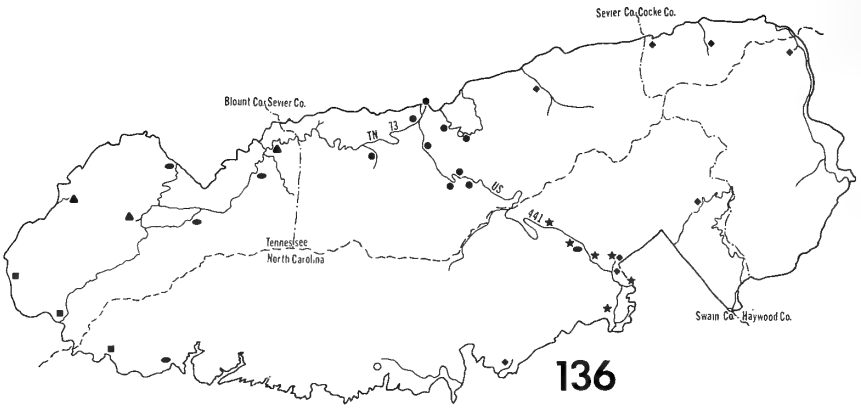


FIG. 136, Distribution of species and subspecies of *Sigmoria* in the Great Smoky Mountains National Park. Diamonds, *rubromarginata rubromarginata;* dots, *bidens;* stars, *tuberosa;* ovals, *translineata;* triangles, *fumimontis;* squares, *lyrea;* circle, *nantahalae.*

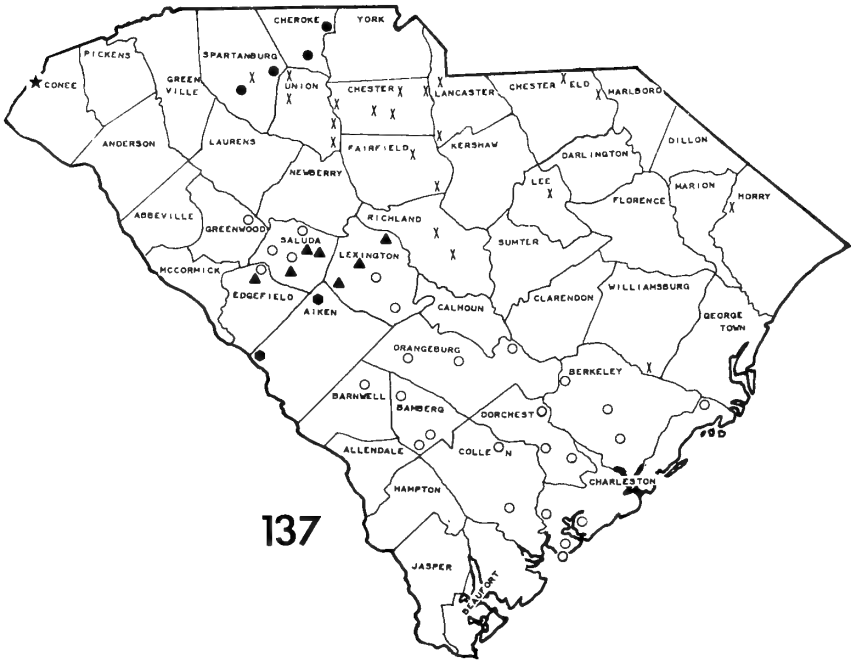


FIG. 137, Distribution of species and subspecies of *Sigmoria* in South Carolina. Dots, *latior munda;* circles, *l. hoffmani;* X's, *latior* intergrades; triangles, *quadrata;* hexagons, *laticurvosa;* star, *disjuncta.*

tergrade area has been expanded into coastal North Carolina, and intergrade records are now available for many inner counties. However, most of the range disparities of *latior* that I cited in 1976 still exist today. The nominate subspecies still has not been collected along the New River in the Ridge and Valley Province of Virginia or in the Tar and Roanoke River basins of piedmont North Carolina or Virginia. With our vastly improved knowledge of the southeastern xystodesmid fauna and the additional material accumulated in the past five years, it appears that the milliped is absent from these areas. The most important distributional changes from 1976 concern the ranges of *l. munda* (formerly *l. mariona*) and *l. latior* in

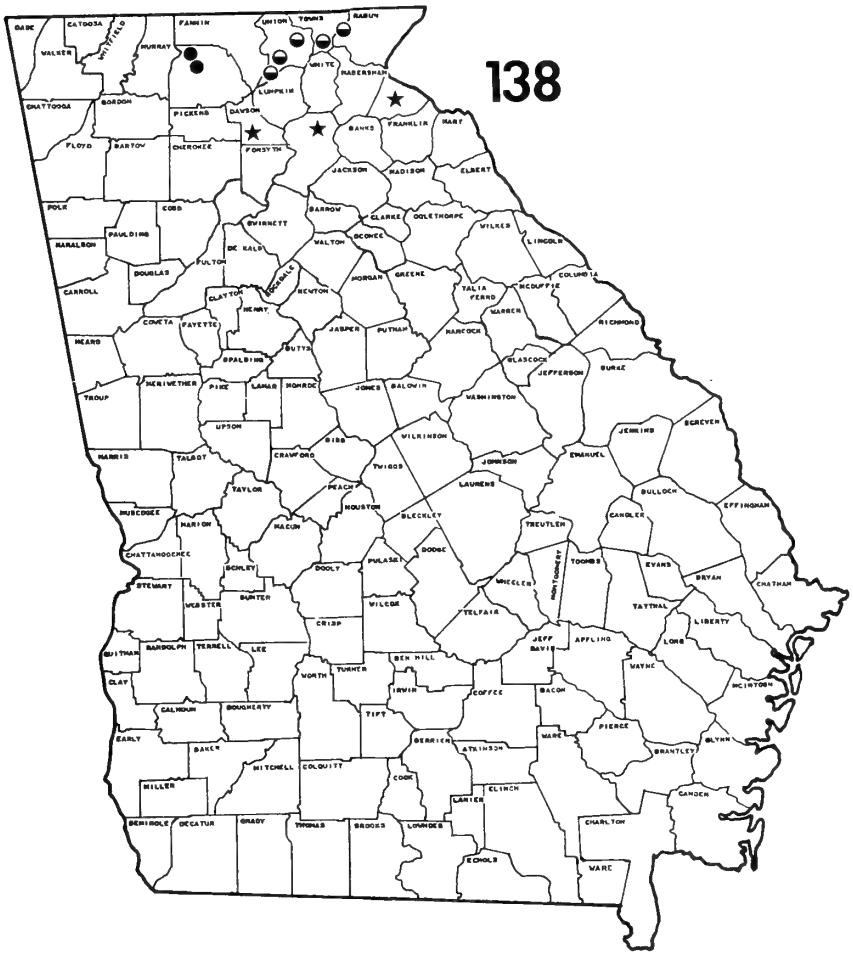


FIG. 138, Distribution of species of *Sigmoria* in Georgia. Dots, *xerophylla;* half shaded dots, *nantahalae;* stars, *disjuncta.*

the North Carolina mountains. Both can now be authentically reported from regions draining to the Tennessee River, in mountains west of the eastern continental divide. The former occurs in Madison, Buncombe, Yancey, Jackson, and Macon counties, North Carolina, and should be expected in Cocke County, Tennessee, since Hot Springs is only a few miles east of the state line. It is rare in these mountains, however, and only encountered sporadically. Field collecting in the Piedmont Plateau also has revealed that *l. munda* occurs much farther east of the mountains than previously thought, as it has been discovered in Rutherford County, North Carolina, and Cherokee and Spartanburg counties, South Carolina. The nominate subspecies has been collected only once in a Tennessee River drainage area of North Carolina, in Mitchell County east of Bakersville, approximately 7 miles N Spruce Pine. Only one individual, an adult male, was encountered, and *l. latior* is even rarer than *l. munda* west of the eastern continental divide.

Thus, *latior* has the largest range by far of any milliped under consideration and one of the largest in the tribe Apheloriini. It is an eminently suc-

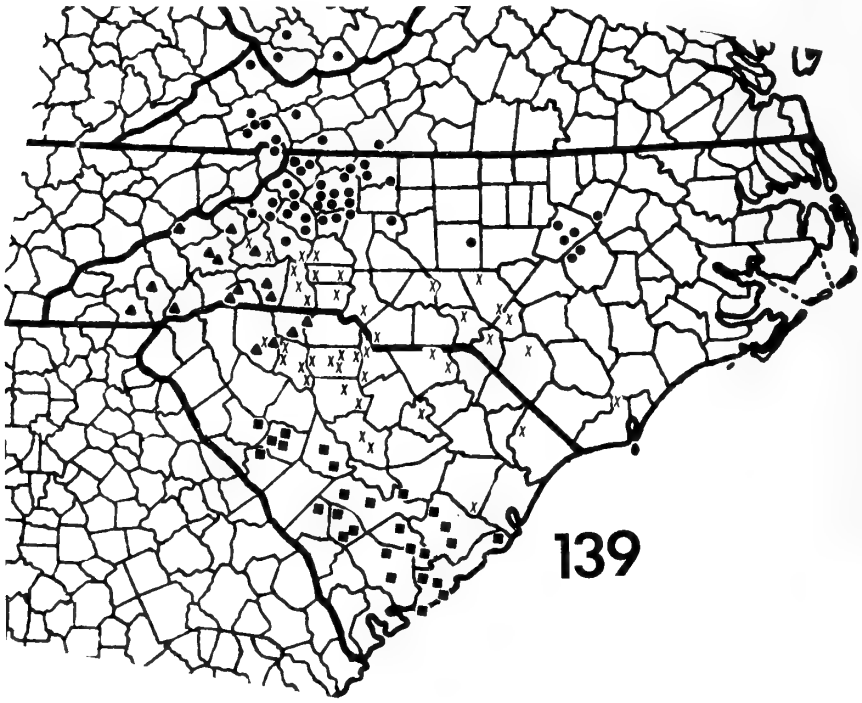


FIG. 139, Distribution of *Sigmoria latior*. Dots, *l. latior;* triangles, *l. munda;* squares, *l. hoffmani;* X's, *latior* intergrades.

cessful milliped as evidenced by its occurrence in five physiographic provinces and by its adaptation to such diverse environments as coastal cypress swamps and climax, montane, deciduous forests. No other species of *Sigmoria* occurs in more than one physiographic province except *rubromarginata,* which inhabits coves in the Blue Ridge Province and the South Mountain inselberg of the Piedmont Plateau. As mentioned in the species account, however, the latter is really an eastward extension of the Blue Ridge.

One interesting situation involving distribution is the fact that distinctive geographic races have evolved for few of the cove inhabiting species. The mountain coves and stream bottom environments are discontinuous, and many such spots in an area seem isolated from each other. Hence, the distributions of the cove species are patchy, as opposed to those of millipeds inhabiting the reasonably continuous climax forests. Since the animals do not seem to wander out of the coves, there appears to be ample opportunity for development of localized gene pools displaying phenotypic differences. However, although considerable phenotypic differences may exist between local populations, the variation in most taxa is random and capricious, and it does not exhibit a geographic pattern. Among the monotypic species, a significant geographic pattern is detectable only in *stibarophalla* and *simplex.* The only polytypic taxa other than *latior* are *rubromarginata,* with widely disjunctive subspecies, and *nigrimontis,* in which differentiation was more localized. Aside from these examples, there are no detectable phenotypic differences in segregated local populations of cove dwelling species that might indicate future evolutionary trends. Differences may exist at the biochemical level, and though not apparent through visual examination might be revealed through more sensitive techniques such as electrophoresis of haemolymph proteins. Or, there might be more contact between neighboring cove populations than thought, thus providing genetic continuity. Whatever the cause, phenotypic and presumably genotypic stability is one of the most notable features of these isolated cove populations.

Conclusion

Normally at this place in a revision I present a statement of generic and specific relationships in which I relate the genus to others in the tribe and discuss affinities among species. The latter, however, have already been indicated by placement of species within the various groups, and inadequate knowledge of other "sigmoid" taxa precludes statements at the generic level. *Sigmoria* is obviously closely related to *Hubroria* and the genus to which *mimetica* belongs, but until these genera and their species have been

adequately diagnosed, attempts to analyze relationships among "sigmoid" taxa are premature. Other undescribed apheloriine genera also bear on this problem as does *Apheloria,* which is currently unrevised. Affinities between species groups of *Sigmoria* are unclear for the same reason; informed judgements about ancestral and derived states for various characters cannot be made due to lack of knowledge of their conditions in related taxa. Thus, discussions of generic and specific relationships are deferred until knowledge of related apheloriine taxa is elevated to a level comparable to that of *Sigmoria.*

Addendum

While the manuscript was in press, two males of *S. l. latior* were discovered in Pulaski County, Virginia, along VA highway 100, 6 miles N Dublin. This record establishes the genus and species in the New River Valley of the Ridge and Valley Province of Virginia, where it was thought to be absent (Shelley 1976, "Distribution" section of this paper), and represents a range extension of some 50 miles from the nearest known locality in Wythe County. The distributional map of *Sigmoria* (Fig. 131) does not reflect this new locality, but it is incorporated into Figure 1 of Shelley (in press). I thank Charles P. Withrow and Barry D. Valentine, who collected the specimens on August 3, 1981.

Acknowledgments

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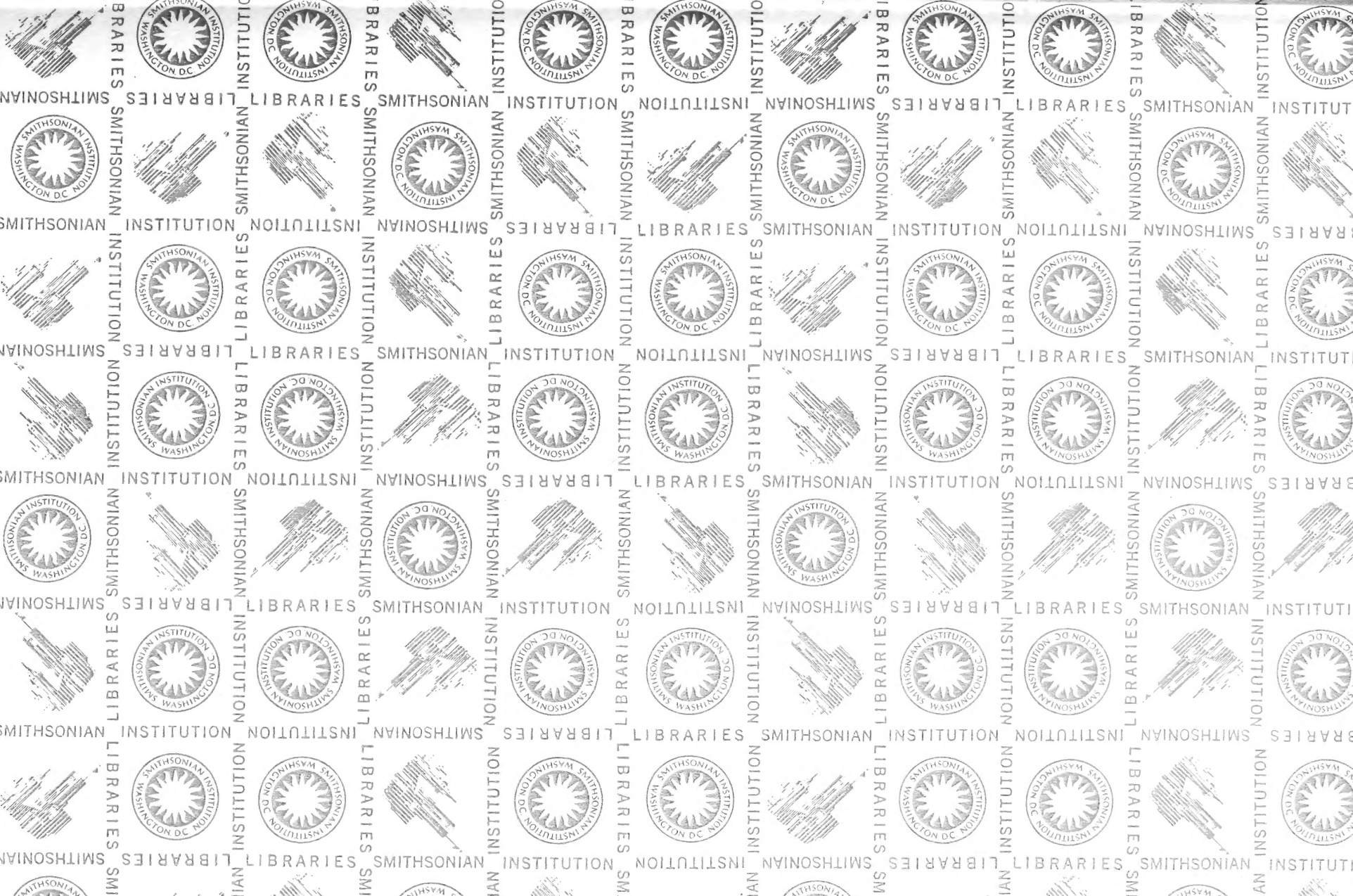
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